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Canada

PRIMARY SUCCESSION FOLLOWING RETREAT OF THE ROBSON GLACIER, BRITISH COLUMBIA

by

DAVID J. BLUNDON

(C)

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH IN

PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

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External Examiner

Date June 7, 1989.

To my parents, Elizabeth and Cyril

ABSTRACT

Primary succession on highly calcareous parent material of the Mount Robson glacial moraines was examined by documenting plant community development as inferred from studying surfaces of different ages, and as observed by redescribing sites previously documented. Vegetation development within moraines was found to be similar to that observed on a chronosequence of moraines. This similarity supports the inferential methods used to study succession at other sites.

The vegetation on the Robson moraines was classified into three phases. The pioneer Hedysarum phase occurred on the youngest recessional moraine (8) and was dominated by the herb Hedysarum boreale var. mackenzii. The Dryas transition phase occurred on recessional moraines 7 and 5 and was dominated by D. drummondii and H. boreale. The oldest successional plant community, the Picea phase, was found on recessional moraines 3, 2, and 1, and the terminal moraine. It was dominated by P. engelmannii and Arctostaphylos rubra.

Importance-value curves for all the communities were essentially linear, fitting the niche preemption model which is typical of species poor-communities controlled by a single factor. This conclusion is also supported by the predominance of negative interspecific associations, which indicates that competition may play an important role in structuring the communities throughout the chronosequence.

The legume Hedysarum boreale was considered the major nitrogen-fixing agent on the moraines, followed by soil microorganisms. The estimated annual N input from biological nitrogen fixation decreased approximately 8-fold over the 200 year forest succession.

Hedysarum boreale formed centres of establishment for Salix

seedlings, and for S. glauca and Picea engelmannii which become dominant species on the older moraines, thus facilitating succession..

During succession, spatial pattern at first intensifies at the scales initially observed, followed by a general reduction in intensity with community development, following the trends suggested by other researchers. However, the number of scales of pattern of each species remained relatively constant and did not decrease on the older moraines.

It is concluded that while the 200 year old vegetation on the Robson moraines is physiognomically mature, it has not attained all the characteristics expected of a fully mature community. Future changes on the Robson moraines may include increased abundance of Abies lasiocarpa and feather mosses together with soil maturation until, in the absence of fire, and other disturbances, the old growth Picea-Abies forest of the subalpine zone is attained.

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1. INTRODUCTION

Ecologists have long recognized the importance of time in the development of plant communities. Long-term studies involving hundreds of years of vegetation change are rare (e.g., Glacier Bay, Alaska). Such studies are typically observations of the change in vegetation on a time sequence of ground surfaces created by, for example, glaciation, mudflows and volcanism. One limitation of the chronosequence or "side-by-side" method of studying vegetation development is the assumption that all the stages of development in the sequence have or will have passed through an identical development sequence (Mueller-Dombois and Ellenberg 1974). This assumption cannot be rigorously proved and is not always thoroughly assessed (Stevens and Walker 1970). The suitability of a chronosequence for the study of plant community development can be best judged from a knowledge of its history of formation and vegetation development. The last advance and retreat of the Robson Glacier (Mount Robson Provincial Park, B.C., Canada) has left a well developed series of moraines beginning in 1783. These moraines have been accurately dated, photographed, and their vegetation and soil development described a number of times since 1914. The Robson moraines thus provide an excellent site at which to study primary succession and the development of subalpine forest ecosystems in western North America.

The goal of this research project was to intensively study temporal vegetation changes on the Robson moraines, and to evaluate potential mechanisms governing rates of succession and spatial pattern development.

Three models of succession, referred to as the facilitatiion, inhibition, and tolerance models, have been proposed by Connell and Slatyer (1977). The facilitation model emphasizes that early colonizers encourage the establishment and growth of later successional species. The facilitation model should be most applicable to primary succession where recruitment could be restricted by limiting physical factors (Connell and Slatyer 1977). The inhibition model states that early colonizers outcompete subsequent colonizers for limited resources and thus discourage rather than encourage, the establishment of later successional species. The tolerance model contends that late colonizers will be able to survive lower levels of resources than early colonists and eventually dominate. Finegan (1984) and Huston and Smith (1987) consider these definitions to be restrictive. Huston and Smith recommend they be viewed as relative, not absolute, mechanisms which "can occur simultaneously, with varying degrees of importance, during every successional sequence".

Huston and Smith (1987) have proposed a model of succession which advocates a reductionist approach emphasizing competitive ability, life history, and physiological traits of individual species, and nonequilibrium processes such as asymmetric competition so that communities do not exist at competitive equilibrium. The Huston and Smith model relies on "nonequilibrium processes, capable of interacting with disturbances to produce steady-state communities whose properties depend on abiotic conditions, such as temperature and resource levels, and on the type and frequency of disturbances". In contrast, Tilman's (1982, 1985, 1988) resource ratio hypothesis of succession relies on population and community attributes, and

equilibrium processes. The resource ratio hypothesis maintains that different colonists are better competitors at certain ratios of resources (e.g., light and nitrogen) and will thus dominate different stages of succession. Tilman (1988) predictd that "long-term, slow changes in resource availabilities (e.g., nitrogen) are likely to be a more important cause of primary succession, and the transient dynamics of competitive displacement are likely to be of greater importance on substrates that are initially more nutrient rich". The resource ratio hypothesis of succession also predicts that "If the rate of accumulation of the limiting soil resource is slow relative to the rate of competitive displacement, many of the features of primary succession might be explained as a slowly shifting trajectory of equilibrium plant communities, with the composition at any point mainly determined by the relative availability of the limiting soil resource and light" (Tilman 1988).

The vegetation present on the 200 year old Robson chronosequence was described and classified in order to gain an understanding of the processes of primary succession on the moraines. Changes in the spatial pattern of colonizers on the moraines were examined to investigate vegetation change and the development of what Sondheim and Standish (1983) refer to as "temporary steady state conditions" on the Robson moraines.

Hedysarum boreale var. mackenzii is an early colonizer and nitrogen-fixing vascular plant on the Robson moraines. The potential role of H. boreale and other possible N-fixers in facilitating colonization through nitrogen fixation was investigated in relationship to community development and the rate of plant succession on the Robson moraines.

1.1 References

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.

Finegan, B. 1984. Forest succession. Nature 312: 109-114.

Huston, M. and T. Smith. 1987. Plant succession: Life history and competition. Am. Nat. 130: 168-198.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, Toronto, Ont. pp 379-380.

Sondheim, M.W. and J.T. Standish. 1983. Numerical analysis of a chronosequence including an assessment of variability. Can. J. Soil Sci. 63: 501-517.

Stevens, P.R. and T.W. Walker. 1970. The chronosequence concept and soil formation. Quart. Review Biol. 45: 333-350.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton Univ. Press, Princeton, N.J. pp 228-234.

Tilman, D. 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125: 827-852.

Tilman, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton Univ. Press, Princeton, N.J. 360 pp.

2. PRIMARY PLANT SUCCESSION ON THE MOUNT ROBSON MORAINES, BRITISH COLUMBIA

2.1 Introduction

Succession trends are generally studied by examining "side-by-side" contemporary communities (i.e., similar sustrates in geographically separate places) (Mueller-Dombois and Ellenberg 1974, p 379). The validity of such successional studies depends on a thorough understanding of the ecology, soils, geology and climate of the entire area studied, and a knowledge of the starting time of successional development. Very few ot these sites have been studied for any length of time or have a well documented written history (Mueller-Dombois and Ellenberg 1974).

Terrestrial primary succession in North America has been well documented (e.g., Cowles 1899; Eggler 1941; Dickson and Crocker 1953; Heusser 1956; Leisman 1957; Lawrence 1958; Olson 1958; Tisdale et al. 1966; Viereck 1966, 1970; Heath 1967; Morrison and Yarranton 1973; Shure and Ragsdale 1977; Birks 1980; Russell and La Roi 1986; Svoboda and Henry 1987; Walker et al. 1986; Fitter and Parsons 1987). However, very few primary succession study areas have a well documented historical record. The Robson moraines in British Columbia are one of the best recorded chronosequences in North America. Originally described and photographed by Cooper (1916) in 1914, the moraines were again described and photographed by Tisdale et al. (1966) in 1963.

The objective of this study was to compare two methods of studying

succession. Primary succession on the Mount Robson glacial moraines was examined by: i) documenting plant community development on surfaces of different ages; and ii) by redescribing sites previously documented. To accomplish these goals, vegetation on the Robson moraines was quantitatively described and classified. Historical documentation of the vegetational development on the moraines was continued by rephotographing areas photographed in 1914 and 1963, thus continuing the work of W.S Cooper and E.W. Tisdale and his associates.

2.2 Study Area

Mount Robson (3954 m) is the tallest mountain in the Canadian Rockies and supports a major ice and snow field. The Robson Glacier, the largest on Mount Robson, has deposited a terminal moraine and approximately 10 recessional moraines during the last 200 years. The Robson moraines (53.1 °N, 119.1 °W) are situated at an elevation of 1662 ± 14 m. The moraines are 1.58, 1.49, 1.45, 1.38, 1.32, 1.17, 0.98, and 0.66 km north-west from the 1984 terminus of the glacier (Figure 2-1). These moraines are referred to as the terminal and recessional moraines 1, 2, 3, 4, 5, 7, and 8, respectively (Heusser 1956). Recessional moraine 6 has been washed away by the Robson River. The terminal moraine was deposited in approximately 1783 while subsequent recessional moraines were formed in approximately 1801, 1864, 1891, 1907, 1912, 1933 and 1939. Dates of formation are based on tree ring counts of the largest trees on each moraine (Heusser 1956), photographic evidence (Wheeler 1932; E.W. Tisdale personal communication), and distance measurements between Robson Glacier and individual moraines (Cooper 1916; Wheeler 1923; Field and Heusser

1954). Luckman (1986) has also reconstructed the 12th/13th century and 'Little Ice Age' glacial advances at Robson.

No climatic data are available for the immediate area of Mount Robson. The nearest climate station is at Red Pass Junction, 20.2 km to the southeast of the mountain at an elevation of 1059 m. Mean daily temperature and mean annual precipitation at this station are 1.7 °C and 742.6 mm. Approximately 54% of the total precipitation occurs as snowfall (Anonymous 1982a, b). The climate at the study site is undoubtedly colder and wetter than that of Red Pass Junction due to greater elevation. The 1985 mean daily air temperature and total precipitation for July and August were 11.1 °C and 16.3 mm and 7.5 °C and 86.1 mm, respectively. The 1986 mean daily air temperature and total precipitation for July were 7.4 °C and 75.5 mm and for August 1-23 were 9.3 °C and 10.5 mm, respectively (see Chapter 6).

Soil development on the moraines was first described by Tisdale et al. (1966) and more recently by Sondheim and Standish (1983). In general, the soils are well drained loams with a 40 to 70% coarse fragment (>2 mm) content. Orthic Regosols occur on the most recently formed moraines while Orthic Eutric Brunisols have developed on the oldest moraines. All the soils are highly calcareous (76-86% $CaCO_3$ equivalent) and slightly alkaline (pH 7.75 to 7.95). On the oldest moraine both soil organic matter and total soil nitrogen content are approximately 10 times greater than they are on the youngest moraine (Sondheim and Standish 1983).

The first recorded description of the Robson moraines was made by Coleman (1910) in 1908. At that time, Robson Glacier extended to the present position of recessional moraine 5. Coleman described the then

youngest moraine (4) as unvegetated with only a few small willow bushes on moraine 3. In 1914 Cooper (1916) visited the site and made the first detailed decription of the vegetation on the Robson moraines. Cooper stated, "The fifth moraine, upon which the ice now rests, is very difficult of access because of the outlet stream, and is probably entirely bare of vegetation." "The fourth, viewed from even a short distance, would also appear to be without plants. Careful search however over a considerable area - an acre or two - revealed the presence of a few scattered individuals - about one hundred in the space examined." (Plates 2-5 and 2-6).

Cooper found moraine 3 (Plate 2-8 and 2-9) to be sparsely but more abundantly vegetated than the 4th moraine. He also recognized the first definite plant community (Dryas octopetala-Arctostaphylos rubra) on recessional moraine 3, although he described it as hardly more than a rudimentary community dominated by herbs and creeping shrubs. On the second recessional moraine, he described two communities, the early successional Dryas-Arctostaphylos community as well as the later successional Salix-Betula glandulosa stage. Cooper also noted the presence of numerous young spruce (Picea engelmannii), less than 1.8 m in height, and a large percentage of bare ground (Plate 2-9).

On recessional moraine 1 and the terminal, Cooper described in some detail the "Climax Forest" stage of vegetation succession on the moraine. This community was an open forest of small Picea engelmannii (<6 m in height) with a dense understory of Salix sp., Betula glandulosa, Shepherdia canadensis, and Juniperus sibirica (= J. communis). In open areas, the Dryas-Arctostaphylos community persisted (Plate 2-11). He stated, "There are frequent small areas,

especially on hillock summits and on the outer slope, that are entirely bare of plants and humus."

Heusser (1956) qualitatively described the vegetation in 1953, but Tisdale et al. (1966) were the first to assess the vegetation on the Robson moraines quantitatively. The pattern of dominant species recognized by Tisdale in 1963 was similar to the trends described by Heusser in 1953. Hedysarum, Dryas, and Salix were dominant on the younger moraines while Salix, Arctostaphylos and Picea were common on the older moraines.

The vegetation in adjacent Jasper National Park, Alberta is predominantly subalpine forest dominated by Picea engelmannii and Abies lasiocarpa with an understory composed of Hylocomium splendens, Pleurozium schreberi (Brid.) Mitt. and Barbilophozia lycopodioides (Holland and Coen 1983, p 164).

2.3 Methods

Field Studies

The vegetation on all the moraines was sampled using a preferential sampling technique (Gauch 1982). A minimum of eight stands (areas of uniform vegetation cover) was sampled on the terminal moraine and each of the recessional moraines 1,2,3,4,5,7, and 8 (Figure 2-1). In addition, four stands of mature forest in the vicinity of the Robson moraines (base of Rearguard Mountain, outcrop adjacent to the moraines, base of Mumm Peak, and near Adolphus Lake) were also sampled. Each stand was sampled using centrally-located nested quadrats. The vegetation was divided into seven layers (Mueller-Dombois and Ellenberg 1974). The tree layer (woody plants

>5 m in height) was sampled with a 10x20 m quadrat. The tall shrub layer (woody plants 2-5 m in height), mid shrub (woody plants 1-2 m in height) and low shrub layer (woody plants 0.1-1 m in height) were sampled with a 5x5 m quadrat. The dwarf shrub layer (woody plants <0.1 m in height) and herb and graminoid layer (all grasses and sedges) were sampled with 5 contiguous 1x1 m quadrats. The lichen and bryophyte layer was sampled with 5 contiguous 0.1x1 m quadrats. Percent crown cover to the nearest 1% was estimated for each species in the appropriate quadrat. Percent cover for litter, bare rock, and bare soil was also estimated in the 1x1 m quadrats. The density (number of stems) of Picea engelmannii was determined in each layer.

Diameter at breast height (dbh) was determined for all P. engelmannii with a dbh >5 cm. The largest P. engelmannii in each stand was cored at 30 cm, aged and corrected for height (Heusser 1956) to estimate the relative age of each stand. Stand age was based on basal ring counts in stands where only P. engelmannii seedlings or shrubs occurred. Basal area estimates were obtained from the dbh data. Sampling was carried out during July 1984.

Species nomenclature followed Moss (1983), Ireland et al. (1980) and Egan (1987).

Sites photographed by Cooper (1916) in 1914 and rephotographed by Tisdale et al. (1966) ir 1963 were located and rephotographed in 1984 with the vital assistance of E.W. Tisdale. Additional sites photographed by Tisdale in 1963 were also located and rephotographed in 1984. A total of 12 photo points were relocated, photographed in both black and white (55 mm) and colour (35 mm) and mapped on to an airphoto. Two recent and previously undocumented recessional moraines

(7 and 8) were also photographed, marked with rock cairns, and mapped (Plate 2-2). Rock cairns were rebuilt, or built if necessary, at all photo points to aid in their future relocation.

Data Analysis

In order to describe and compare the vegetation on the moraines, stands were classified into community types (recognizable communities characterized by a distinctive species assemblage (Gauch 1982)) using both agglomerative (Pielou 1984) and divisive (Hill 1979) methods. The classification analysis was applied to all the stands (n=73) using species cover data in the 5x5 m quadrats. Community Types (CT's) were given binomial names using the two most abundant species in the community.

For each CT, three indices of alpha diversity (Whittaker 1972) were calculated:

1) Shannon-Wiener Index (Shannon and Weaver 1949)

$$H' = -\sum_{i=1}^{S} (Ni/N)[Ln(Ni/N)]$$

where Ni is the estimated cover of species i in the stands, N is the total cover of all species and S is species richness or the number of species present. The Shannon-Wiener Index is dependent both on the number of species and evenness of cover among species.

2) Species evenness (Pielou 1974)

$$J' = H'/Ln(S)$$

where Ln(S) is the maximum possible diversity for a CT.

3) Species dominance was calculated by means of Simpson's Index

(Simpson 1949):

$$C = \sum_{i=1}^{S} (Ni/N)^2$$

Simpson's Index is a measure of the concentration of dominance using species cover estimates.

Community structure was also examined by constructing species 'importance-value' curves (Whittaker 1972). In addition, species structure slope angles (A) and coefficients of determination (r^2) were calculated for each importance-value curve (Purchase and La Roi 1983) as a test of their fit to the geometric, lognormal and broken-stick community structure models (Whittaker 1972). The species structure curves were also fitted to the lognormal distribution.

2.4 Results

Historical Evidence

On newly exposed surfaces (recessional moraine 4) which had been ice-free for approximately 10 years, Cooper (1916) found the following colonizers: Salix seedlings, Epilobium latifolium, Castilleja pallida (= C. occidentalis), Saxifraga aizoides, Lychnis apetala, and a single seedling of Picea engelmannii. Salix seedlings, Epilobium latifolium and Saxifraga aizoides were also found colonizing newly exposed surfaces in 1984. Castilleja occidentalis and P. engelmannii were found on surfaces approximately 30 years old, while Bryum sp. and Dryas drummondii were found on surfaces less than 20 years old.

The dominant species found on each moraine in 1984 are listed in Table 2-1 for comparison with the earlier studies. Comparisons can be made within and between moraines, especially within the last 77 years

(moraines 4, 5, and 8), which show that comparable sequences of plant community development have occurred on these surfaces. For example, vegetation development on recessional moraine 2 in 1914 (Plate 2-9) is similar to that on moraine 4 in 1963 (Plate 2-5), moraine 5 in 1963 (Plate 2-4), and on recessional moraine 7 in 1984 (Plate 2-3). At the time they were described these four surfaces were 50, 56, 51, and 51 years old, respectively. Vegetational development on moraine 3 in 1963 (Plate 2-7) was similar to that on moraine 5 in 1984 (Plate 2-4). These surfaces were approximately 73 and 72 years old, respectively. This similarity supports the inferential methods used to study succession at other sites.

Classification of Communities

The results of an agglomerative, metric, weighted, group average clustering analysis employing Ruzicka's Index of Similarity (Pielou 1984) are shown in Figure 2-2. Five community types (CT's) were recognized.

HEDYSARUM-SALIX Community Type

The HEDYSARUM-SALIX CT (6 stands) occurred only on moraine 8, the youngest surface sampled (Figure 2-2). It occurred on level ground and undulating surfaces with slopes less than 15% inclination. Total plant cover was 11% (±2) with rock and soil dominating the ground surface (Table 2-2 and Plate 2-3).

Structurally, the HEDYSARUM-SALIX CT was a herb-dwarf shrub community co-dominated by the herb Hedysarum boreale var. mackenzii and several species of Salix (S. vestita, S. alaxensis and S. glauca) (Table 2-2). This community had the lowest species richness (26) of

the 5 CT's (Table 2-3). Stand age varied from 2 to 20 years with a mean of 11 years.

SALIX-DRYAS Community Type

The SALIX-DRYAS CT (7 stands) was well represented on moraine 7 (Plate 2-3) with one stand located on moraine 5 (Figure 2-2). It occurred on level ground and north- and northwest-facing slopes (1-6% inclination). Plant cover averaged 49% (±4) with litter having a total cover of 47%.

This CT was dominated by low and dwarf shrubs (Table 2-2). Picea engelmannii crowns were beginning to emerge from the low shrub layer (<1 m) (Plate 2-3). Salix glauca, S. vestita and S. ferriae were dominant shrubs, while the dwarf-shrub layer was dominated by Dryas drummondii, D. integrifolia and D. octopetala. Hedysarum boreale var. mackenzii and bryophytes, especially Brachythecium spp. (e.g., B. groenlandicum (C. Jens.) Schljak.), were also abundant in this community (Table 2-2). Stand age varied from 18 to 33 years with a mean of 26 years.

DRYAS-HEDYSARUM Community Type

The DRYAS-HEDYSARUM CT (17 stands) occurred primarily on moraines 4 and 5 (65% of the stands) with the remaining stands on moraines 8 and 7 and one on moraine 3 (Figure 2-2). It occurred predominantly on slopes of 4-46% inclination with varying aspects. Vegetation cover was somewhat higher than that found in the younger SALIX-DRYAS CT with a total plant cover of 58% (±4).

The DRYAS-HEDYSARUM CT was structurally a dwarf shrub-herb community with an emergent tall shrub layer (2-5 m) of Picea

engelmannii (Table 2-2 and Plate 2-4). It was co-dominated by Dryas drummondii and Hedysarum boreale var. mackenzii. Salix glauca, S. vestita, and bryophytes, especially Brachythecium spp. (e.g., B. groenlandicum and B. turgidum (C.J. Hartm.) Kindb.), were also abundant in this community. Stand age varied from 6 to 82 years with a mean of 50 years.

PICEA-SALIX Community Type

The PICEA-SALIX CT (20 stands) was primarily found on moraines 3 and 4 (75% of the stands) with the remaining stands on moraines 2 and 5 (Figure 2-2). It occurred most commonly on north- and northwest-slopes (4-35% inclination). Total plant cover (73% ±2) was the highest of the 5 CT's studied.

Picea engelmannii and several species of Salix (S. glauca, S. barclayi and S. vestita) co-dominated this shrub community (Plates 2-5 and 2-7). Arctostaphylos rubra dominated the dwarf shrub layer and Hedysarum boreale var. mackenzii the forb layer. Bryophytes, mostly Brachythecium spp., were also abundant (Table 2-2). Stand age ranged from 65 to 188 years with a mean of 86 years.

PICEA-ARCTOSTAPHYLOS Community Type

The PICEA-ARCTOSTAPHYLOS CT (21 stands) occurred primarily on recessional moraine 1 and the terminal moraine (76% of the stands) with the remaining stands on moraine 2 (Figure 2-2). It occurred predominantly on level ground and undulating surfaces with slopes of less than 32% inclination. Total plant cover (65% ±2) was slightly less than that found in the younger PICEA-SALIX CT.

Structurally, the PICEA-ARCTOSTAPHYLOS CT was a forest co-

dominated by Picea engelmannii and Arctostapylos rubra (Plates 2-10 and 2-11). Cladonia cariosa and C. pyxidata dominated the lichen layer. Bryophytes, especially Brachythecium sp., were also abundant (Table 2-2). This CT had the highest species richness (70) of the 5 CT's (Table 2-3). Stand age varied from 115 to 234 years with a mean of 166 years.

According to the vegetation classification of Holland and Coen (1983, p 70), this CT was floristically similar to a Picea engelmannii-Abies lasiocarpa open-forest vegetation type (012).

Diversity

Species richness increased with stand age in the bryophyte, lichen and herb layers and declined slightly with age in the dwarf shrub layer. In the shrub layer, species richness reached a peak in the intermediate DRYAS-HEDYSARUM CT (Table 2-3). Cover in the lichen and tree layers, was highest in the oldest stage of community development (PICEA-ARCTOSTAPHYLOS CT). Bryophyte cover reached a peak in the late successional PICEA-SALIX CT. Herb and dwarf shrub cover peaked in the intermediate DRYAS-HEDYSARUM CT. Shrub cover changes were erratic with a major peak in the late successional PICEA-SALIX CT (Table 2-3).

In general, community diversity (Shannon-Wiener Index) increased with increasing age except for a drop in the intermediate DRYAS-HEDYSARUM CT (Table 2-3). Community evenness varied little between CT's and was lowest in the DRYAS-HEDYSARUM CT. Dominance (Simpson's Index) was highest in the pioneer HEDYSARUM-SALIX CT and intermediate DRYAS-HEDYSARUM CT. Species structure slope angles generally declined with increasing age (Table 2-3 and Figure 2-3). Coefficients of

determination for the CT's were high for a linear fit, ranging from Ø.943 to Ø.986, which imply a better fit to the geometric series than to alternative models. The importance-value curve of the PICEA-ARCTOSTAPHYOS CT was also fitted to a lognormal distribution and found to be significantly different ($p<.ØØ1$) from it when compared with a G-test (Sokal and Rohlf 1981).

Picea engelmannii Density and Basal Area

There was no clear trend in Picea engelmannii density with increasing community age (Table 2-4). Peak densities occurred in the early SALIX-DRYAS and the late PICEA-SALIX CT's with a low in the intermediate DRYAS-HEDYSARUM CT. The proportion of Picea engelmannii in the dwarf shrub layer (seedlings) decreased with increasing community age to a low in the late PICEA-SALIX CT and then increased dramatically in the oldest CT. The proportion of Picea engelmannii in the shrub layer increased with increasing community age to a peak in the late PICEA-SALIX CT. Total basal area increased with stand age (Table 2-4). Total basal area in the late successional PICEA-ARCTOSTAPHYOS CT was 19.1 ± 2.6 m^2 ha^{-1} on recessional moraine 1 and 18.3 ± 3.1 m^2 ha^{-1} on the terminal moraine. Only a few fallen trees and exposed mineral soil were seen on the oldest moraine and no evidence of fire was noted.

Picea engelmannii-Abies lasiocarpa Subalpine Forest

Mature stands sampled in the vicinity of the Robson moraines are comparable to vegetation types C13 and C14 described in Holland and Coen (1983, p 51 and 52) for Jasper National Park, Alberta, with the exception of the Picea-Abies stand on a rock outcrop adjacent to the

terminal moraine, which was a C24 vegetation type (Holland andCoen (1983, p 58). These areas have been ice free for at least four centuries (Heusser 1956). Heusser described the vegetation on the outcrop as part of the "ancient" forest which was not overrun by ice in the last advance. The largest tree in the rock outcrop stand was dated to be 368 years old. Species richness (S=64), diversity (H'=2.32) and evenness (J'=Ø.554) of the four mature stands were somewhat lower than those found for the late successional PICEA-ARCTOSTAPHYLOS CT on the moraines (Table 2-3). The average total basal area of the four stands was, however, 40.0 ± 7.0 m^2 ha^{-1}, more than twice that of the PICEA-ARCTOSTAPHYLOS CT.

A fire swept through at least the western part of the valley before 1914 (unpublished photograph of a burn on the northwest shore of Berg Lake taken by W.S. Cooper in 1914). Evidence of fire was also noted in the rock outcrop stand.

2.5 Discussion

Past and current research indicates that the same species have been available for colonization on the Robson moraines for the last 77 years at least. Thus, the sequence of community development on the younger moraines was probably similar to that on the older moraines. A comparison of photographs taken in 1914, 1963, and 1984 of the Robson moraines also supports this conclusion. Future trends in community development, may of course, be different.

Three phases of vegetation development can be recognized on the Robson moraines based on plant community structure and age. These phases are represented on the dendrogram of clustered stands as three

distinct groups that fused at a similarity index of approximately 26% (Figure 2-2). The pioneer Hedysarum phase (45 years) is represented by the HEDYSARUM-SALIX CT on moraine 8. In this phase, vegetation cover was sparse and the ground surface was predominantly bare rock and soil. The Dryas transition phase (51-72 years) was represented by the SALIX-DRYAS and DRYAS-HEDYSARUM CT's on moraines 7 and 5. Hedysarum and Salix were predominant but Dryas drummondii attained its peak cover during this phase. Vegetation cover increased dramatically at this phase from the pioneer phase of succession. Picea engelmannii emerged from the mid-shrub layer but its cover was low. The Picea phase (93-201 years) represented the final stage of plant community development on the moraines and was represented by the PICEA-SALIX and PICEA-ARCTOSTAPHYLOS CT's on moraines 3, 2, and 1 and the terminal. Picea engelmannii was the dominant species and forms the tree layer. Abies lasiocarpa and Pinus albicaulis also occupied the tree layer but were sporadic in cover. A dramatic increase of Arctostaphylos rubra, bryophytes, and lichens was also evident during this late stage of vegetation development.

These major differences in vegetation development reflect a continuum of species abundance on the 200 year-old chronsequence and do not represent sharp changes in vegetation between the moraines. Many of the colonizers which dominate the late successional CT's are also present in the pioneer CT's.

At Glacier Bay, Alaska (59 °N, 136.5 °W), three stages of vegetation development following ice recession have also been described (Cooper 1923; Crocker and Major 1935): a pioneer Alnus stage first dominated by Dryas drummondii and Salix and then by an ALNUS-

SALIX CT; a transition stage (100 years) distinguished by the emergence of Populus balsamifera and Picea sitchensis, and finally a dense cover of Picea sitchensis 170 years after ice melt. Birks (1980) described a successional sequence following the retreat of Klutlan Glacier, Yukon Territory (61 °N, 141 °W), that progressed from bare ground through either a Hedysarum-Salix or a Dryas drummondii stage (10-30 years) to a Salix-Picea transition stage (60-175 years) and finally a Picea glauca stage (175-250 years). The rates of vegetation development at Glacier Bay, the Klutlan Glacier, and the Robson moraines are comparable (Birks 1980). At all three sites, spruce forest development occurred within 100 years of initial colonization. With respect to early successional trends, all three areas were colonized by Dryas drummondii and Salix. Hedysarum boreale was an important early colonizer at the Klutlan Glacier and Mount Robson, both continental sites, but not at Glacier Bay which is maritime. Mosses are important early colonizers at Glacier Bay but are predominant only in the late stages of succession at the continental sites (see 4 old-growth stands in Appendix 2).

In general, indices of species evenness changed little over the 200 years of vegetation development on the Robson moraines except for a drop in the DRYAS-HEDYSARUM CT. This drop was related to a decrease in diversity caused by the dominance of Dryas and Hedysarum. A similar trend was found by Reiners et al. (1971) and Birks (1980) for early successional Dryas-dominated communities. However, species diversity increased with age, except in the DRYAS-HEDYSARUM CT, on the Robson moraines but remained relatively constant both at Glacier Bay (Reiners et al. 1971) and at the Klutlan moraines (Birks 1980) over a

comparable period of succession. This general increase in species diversity can be attributed to the increase in species richness in 200 year old sites (70 species) which was greater than that found at Glacier Bay (38 species) or the Klutlan Glacier (38 species).

Importance-value curves for the Mount Robson chronosequence were similar to those found at Glacier Bay by Reiners et al. (1971). There was a general decline in the slope angle of the curves with increasing age, which is indicative of increasing species richness. All the curves were essentially linear, thus fitting the geometric or niche preemption model (Pielou 1975). Such communities are usually species-poor with a few dominant species preempting a large proportion of a limiting resource (Pielou 1975), and are typical of communities controlled by a single factor (e.g., polluted environments) (Giller 1984).

The PICEA-ARCTOSTAPHYLOS CT on the oldest moraines is similar floristically and physiognomically to the Picea-Abies forest on an outcrop adjacent to the terminal moraine. The vegetation on the outcrop is comprised of species which are prevalent in the surrounding old-growth stands, but are either absent on the Robson moraines (e.g., Cornus canadensis L.) or very sporadic in cover (e.g., Abies lasiocarpa and Barbilophozia lycopodioides). Pleurozium schreberi (Brid.) Mitt., a common subalpine forest species, has not colonized either the outcrop community or Robson moraines. The next phase of "ecosystem development" (Odum 1969) on the Robson moraines may be the colonization and eventual establishment of this group of species during another long and more protracted phase of pattern development.

Species diversity indices of the old-growth forest were lower than

those found on the oldest plant community on the moraines. These trends agree with Margalef's (1958), Grime's (1979) and Huston's (1979) predictions, and evidence provided by Loucks (1970), that plant diversity should show an initial increase during succession followed by a slow decline.

Figure 2-1. Map of the Robson moraines showing the approximate age of the deposits in 1984 and the locations of stands used in the classification analysis. The location of sample sites on surfaces less than 45 years old are shown as unlabeled dots. The cross-section (below) is drawn along the survey line and shows the moraines in exaggerated relief. (RM = recessional moraine, T = terminal moraine) (see panorama photo in Appendix 1)

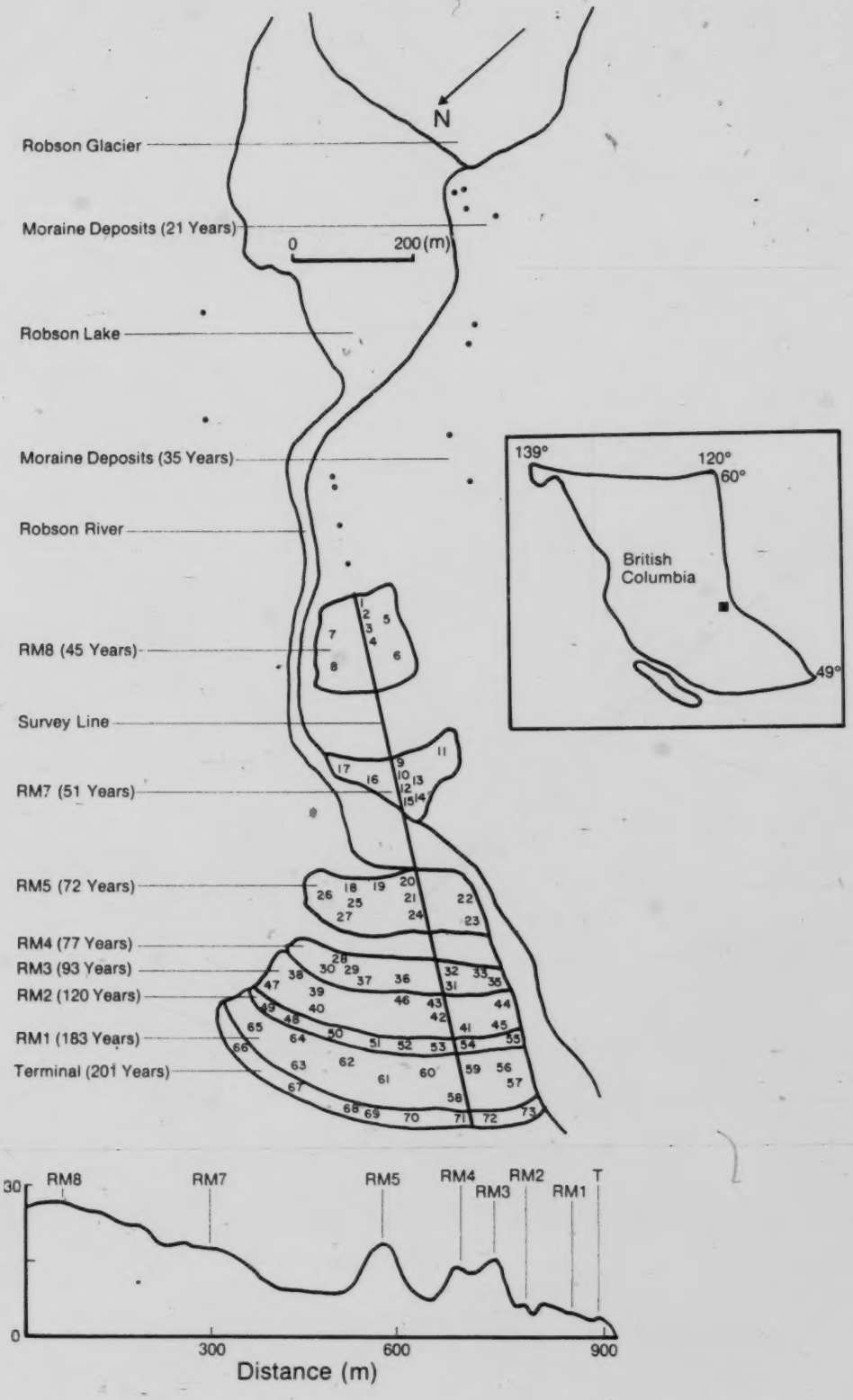
N
Robson Glacier
Moraine Deposits (21 Years)
0
200 (m)
Robson Lake
Moraine Deposits (35 Years)
Robson River
RM8 (45 Years)
Survey Line
RM7 (51 Years)
RM5 (72 Years)
RM4 (77 Years)
RM3 (93 Years)
RM2 (120 Years)
RM1 (183 Years)
Terminal (201 Years)
139°
120°
60°
British Columbia
49°
RM8
RM7
RM5
RM4
RM3
RM2
RM1
T
Elevation (m)
30
0
300
600
900
Distance (m)

Figure 2-2. Dendrogram derived from a weighted, average linkage, agglomerative analysis applied to quantitative plant cover data. Five community types were recognized at the level of the dashed line, and are arranged in increasing age from left to right. Stands 58 and 70 were considered outliers and were not included in the community descriptions. (T = terminal moraine)

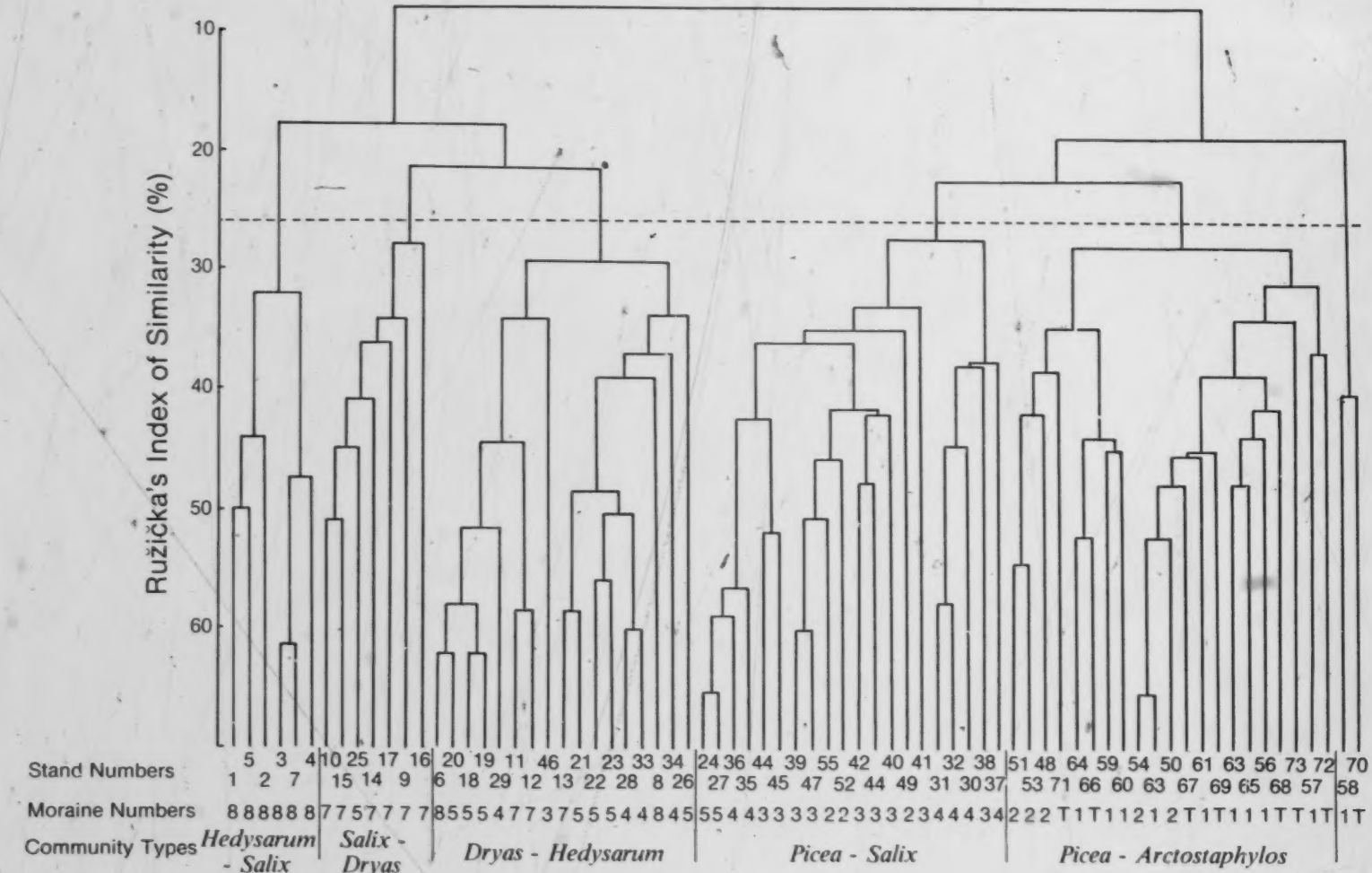
Ružička's Index of Similarity (%)
10
20
30
40
50
60
Stand Numbers
5 3 4 10 25 17 16 20 19 11 46 21 23 33 34 24 36 44 39 55 42 40 41 32 38 51 48 64 59 54 50 61 63 56 73 72 70
1 2 7 15 14 9 6 18 29 12 13 22 28 8 26 27 35 45 47 52 44 49 31 30 37 53 71 66 60 63 67 69 65 68 57 58
Moraine Numbers
8 8 8 8 8 7 7 5 7 7 7 7 8 5 5 5 4 7 7 3 7 5 5 5 4 4 8 4 5 5 5 4 3 3 3 3 2 2 3 3 3 2 3 4 4 4 3 4 2 2 2 T 1 T 1 1 2 1 2 T 1 T 1 1 1 T T 1 T 1 T
Community Types
Hedysarum - Salix
Salix - Dryas
Dryas - Hedysarum
Picea - Salix
Picea - Arctostaphylos

Figure 2-3. Importance-value curves for the five plant community types arranged in order of increasing age from left to right. The community types are; (1) HEDYSARUM-SALIX (n=6), (2) SALIX-DRYAS (n=7), (3) DRYAS-HEDYSARUM (n=17), (4) PICEA-SALIX (n=20), and (5) PICEA-ARCTOSTAPHYLOS (n=21).
(n = number of stands)

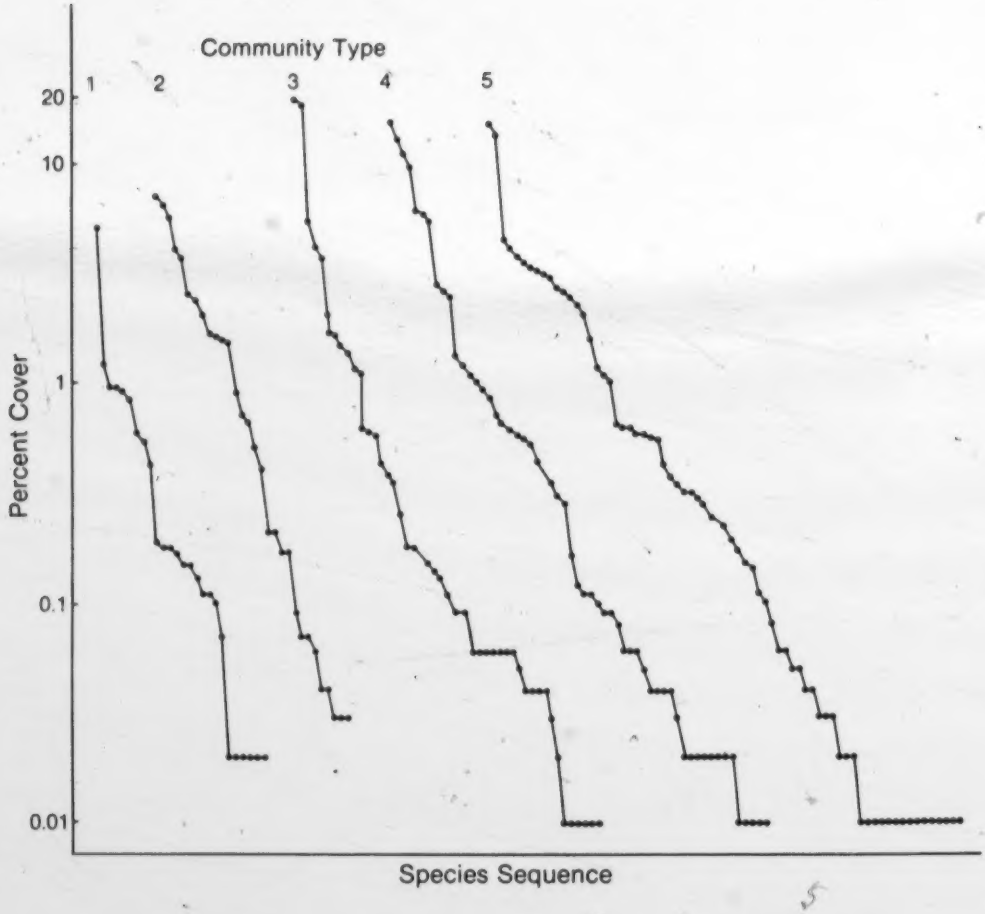
Community Type
1
2
3
4
5
20
10
1
0.1
0.01
Percent Cover
Species Sequence

Plate 2-1. View of the Robson Glacier and moraines taken in 1908 (top) by Rev. G. B. Kinney (Kinney 1909) and in 1984 (bottom) from the slopes of Mumm Peak.

Plate 2-2. Aerial view of the Robson Glacier and moraines (Province of British Columbia aerial photograph, Flight Line BC7515, flown Aug.3, 1973) showing the location of photograph points (FP).

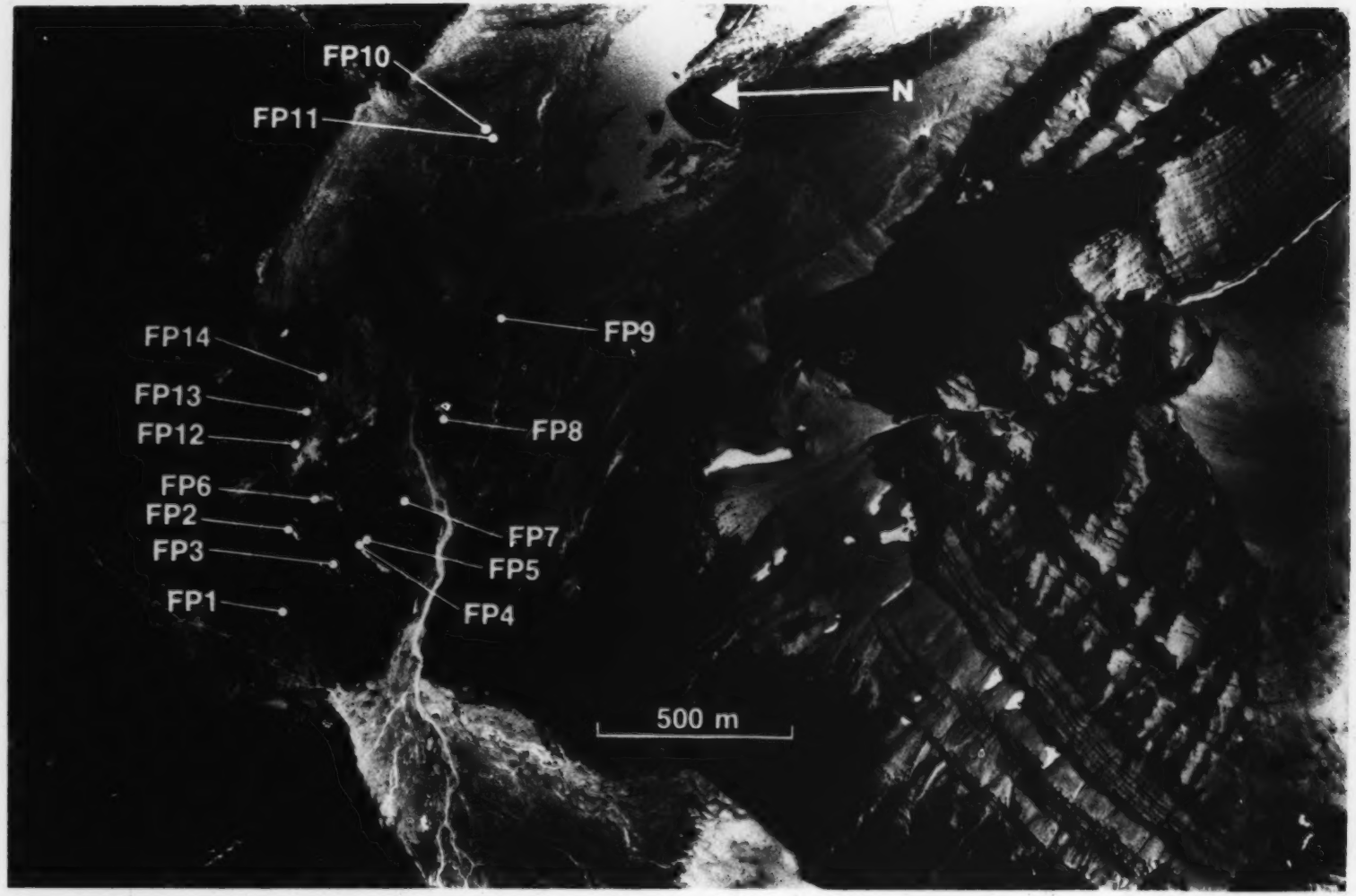
FP10
FP11
N
FP14
FP9
FP13
FP12
FP8
FP6
FP2
FP7
FP3
FP5
FP1
FP4
500 m

Plate 2-3. Northwest looking views of recessional moraine 8 (above) and recessional moraine 7 (below) from photo points FP9 and FP8, respectively (1984). The HEDYSARUM-SALIX CT (youngest) is shown above and SALIX-DRYAS and DRYAS-HEDYSARUM CT's below.

Plate 2-4. Northwest looking view of recessional moraine 5 in 1963 (above), and in 1984 (below) from photo point FP7. The DRYAS-HEDYSARUM and PICEA-SALIX CT's are predominant on moraine 5 in 1984 (below).

Plate 2-5. Southwest looking view of recessional moraine 4 in 1914 (above), 1963 (middle), and 1984 (below) from a marker cairn near its east end (FP5). Note that the top of the crevasse dump in the foreground was still bare of vegetation in 1984. DRYAS-HEDYSARUM and PICEA-SALIX CT's predominated on moraine 4 in 1984 (below).

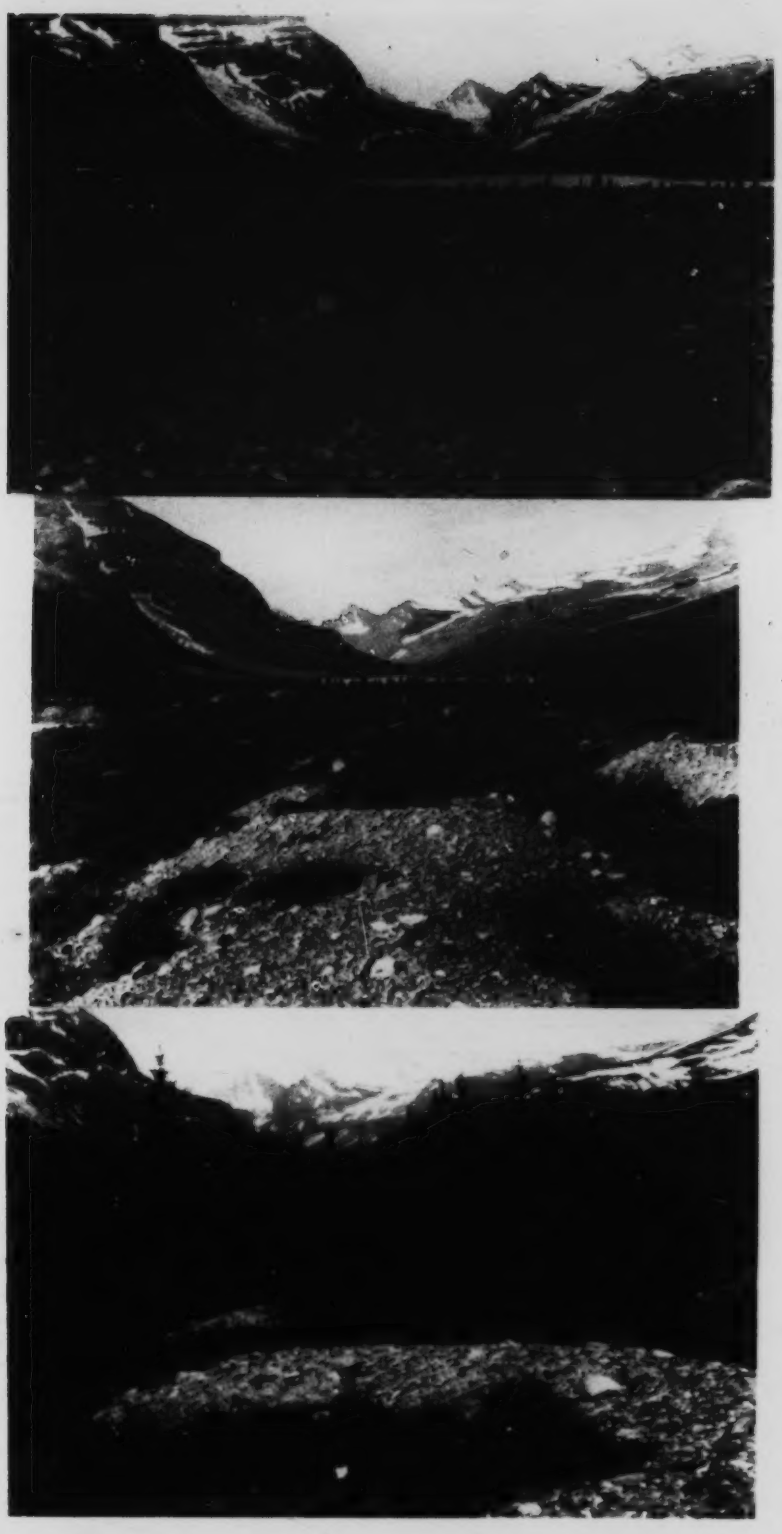

Plate 2-6. General view of the outer northwest slope of recessional moraine 4 and the intermoraine between recessional moraines 4 and 3 in 1914 (above), 1963 (middle), and 1984 (below). The top of recessional moraine 4 was virtually bare of vegetation in 1914. The depression has remained relatively bare of vegetation due to late snow accumulation. This photo point was labeled FP4 on Plate 2-2.

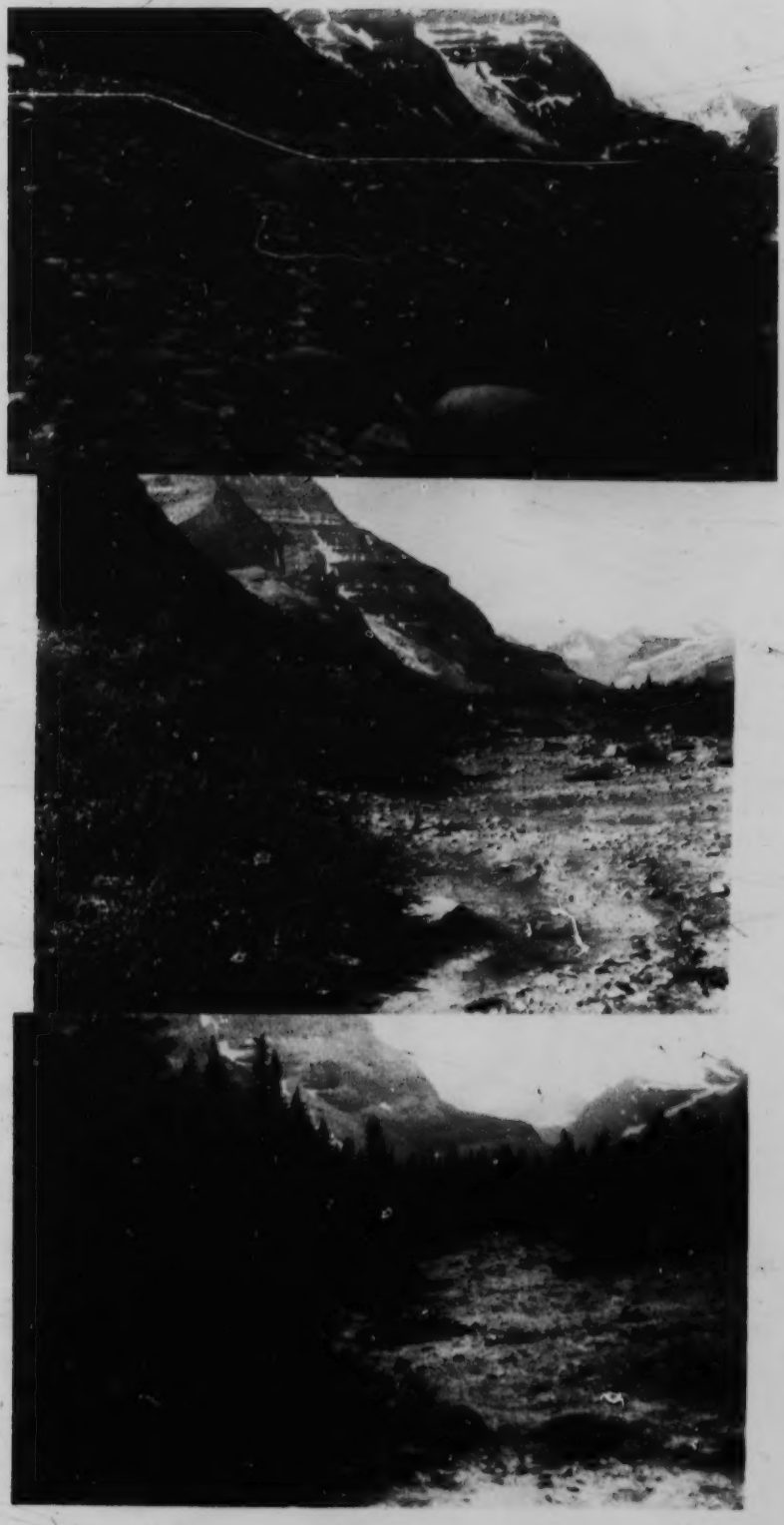

Plate 2-7. Southwest looking view of recessional moraine 3 in 1963 (above) and in 1984 (below) from photo point FP6. The PICEA-SALIX CT was predominant on moraine 3 in 1984.

Plate 2-8. Depression between recessional moraines 2 and 3 in 1914 (above), 1963 (middle), and 1984 (below). Recessional moraine 3 is in the background. The intermoraine vegetation was still quite open compared to the adjacent moraines. This photo point was labeled FP3.

Plate 2-9. Recessional moraine 2 in 1914 (above) and 1963 (below). Recessional moraine 3 is in the background. Note the lack of vegetation on recessional moraine 3 in 1914. This photo point was not relocated in 1984.

Plate 2-1Ø. Depression between recessional moraines 1 and 2 in 1914 (above), 1963 (middle), and 1984 (below). The intermoraine vegetation in 1984 was still quite open compared to the adjacent moraines. This photo point was labeled FP2.

Plate 2-11. General view of the terminal moraine in 1914 (above), 1963 (middle), and 1984 (below) from outwash in front of the moraines (FPl). Note how close the glacier was to the terminal moraine in 1914 (above).

Table 2-1. Descriptions of the vegetation on each Robson moraine in 1914 (Cooper 1916), 1953 (Heusser 1956), 1963 (Tisdale et al. 1966) and in 1984 (RM = recessional moraine)

Moraine	Year of Deposit	Year of Description			
		1914	1953	1963	1984
Terminal	1783	Picea-Salix-Betula	Picea-Arctostaphylos-Salix	----------	Picea-Arctostaphylos-Shepherdia
RM 1	1801	----------	Salix-Betula-Arctostaphylos	Salix-Arctostaphylos-Picea	Picea-Arctostaphylos-Salix
RM 2	1864	Salix-Betula	Salix-Dryas-Arctostaphylos	----------	Picea-Arctostaphylos-Salix
RM 3	1891	Dryas-Arctostaphylos	Hedysarum-Salix-Dryas	Hedysarum-Salix-Dryas	Picea-Hedysarum-Salix
RM 4	1907	Sparse	Hedysarum-Salix	----------	Hedysarum-Salix-Arctostaphylos
RM 5	1912	Bare/Ice	Hedysarum-Salix-Dryas	Hedysarum-Salix-Dryas	Hedysarum-Dryas-Salix
RM 8	1939	Ice	Sparse	----------	Hedysarum-Dryas-Salix

Table 2-2. Mean percentage cover (± standard error) of the species found in each successional community type on the Robson moraines (P < 0.1% cover).

LAYER AND SPECIES	COMMUNITY TYPE				
	HEDYSARUM-SALIX (n=6)	SALIX-DRYAS (n=7)	DRYAS-HEDYSARUM (n=17)	PICEA-SALIX (n-20)	PICEA-ARCTOSTAPHYLOS (n=21)
TREE LAYER					
Picea engelmannii Parry ex Engelm.	-	-	-	1.8 (0.8)	11.5 (1.3)
Pinus albicaulis Engelm.	-	-	-	-	0.1 (0.1)
Abies lasiocarpa (Hook.) Nutt.	-	-	-	-	0.1 (0.1)
TALL SHRUB LAYER					
Picea engelmannii	-	-	2.0 (0.8)	10.1 (1.7)	2.3 (0.8)
Salix farriae Ball	-	-	-	0.4 (0.4)	-
Salix glauca L.	-	-	-	0.1 (0.1)	-
Salix alaxensis (Anderss.) Coville	-	-	-	0.1 (0.1)	0.1 (0.1)
Pinus albicaulus	-	-	-	-	0.1 (0.1)
Pinus contorta Loudon	-	-	-	-	P
Betula glandulosa Michx.	-	-	-	-	P
MID SHRUB LAYER					
Salix alaxensis	0.3 (0.2)	-	0.1 (0.1)	0.2 (0.1)	0.2 (0.1)
Salix glauca	0.1 (0.1)	-	P	0.5 (0.2)	0.6 (0.2)
Picea engelmannii	-	1.9 (1.1)	1.2 (0.3)	3.0 (0.9)	0.4 (0.1)
Betula glandulosa	-	-	0.1 (0.1)	0.2 (0.1)	2.8 (0.9)
Salix vestita Pursh	-	-	-	0.1 (0.1)	-
Salix barclayi Anderss.	-	-	-	0.3 (0.2)	0.5 (0.2)
Shepherdia canadensis (L.) Nutt.	-	-	-	0.1 (0.1)	0.4 (0.2)
Salix farriae	-	-	-	-	P

Table 2-2. Continued

LAYER AND SPECIES	COMMUNITY TYPE				
	HEDYSARUM-SALIX	SALIX-DRYAS	DRYAS-HEDYSARUM	PICEA-SALIX	PICEA-ARCTOSTAPHYLOS
LOW SHRUB LAYER					
Salix arctica Pallas.	0.1 (0.1)	0.1 (0.1)	-	-	-
Salix brachycarpa Nutt. spp. brachycarpa	0.1 (0.1)	-	0.1 (0.04)	-	-
Salix myrtillifolia var. cordata (Anderss.) Dorn	0.2 (0.1)	0.5 (0.2)	0.2 (0.1)	P	-
Populus balsamifera L.	0.1 (0.1)	-	0.1 (0.1)	P	-
Abies lasiocarpa	0.1 (0.1)	0.2 (0.1)	0.1 (0.1)	0.3 (0.2)	-
Salix alaxensis	0.4 (0.2)	0.1 (0.1)	0.5 (0.2)	0.2 (0.1)	0.1 (0.1)
Salix ferrisae	0.4 (0.1)	2.4 (1.1)	0.6 (0.2)	0.8 (0.4)	0.2 (0.1)
Salix glauca	0.6 (0.2)	6.4 (1.0)	5.4 (1.0)	5.6 (0.6)	1.8 (0.4)
Salix vestita	0.6 (0.2)	4.2 (1.2)	1.4 (0.4)	2.5 (0.5)	1.1 (0.3)
Salix barclayi	0.2 (0.2)	1.6 (0.9)	0.4 (0.2)	2.4 (0.6)	1.5 (0.4)
Picea engelmannii	0.3 (0.1)	1.5 (1.1)	0.8 (0.2)	0.7 (0.2)	0.2 (0.1)
Salix barrattiana Hook.	-	0.2 (0.2)	0.1 (0.04)	P	0.1 (0.03)
Salix arbusculoides Anderss.	-	-	P	-	-
Salix scouleriana Barr. ex Hook.	-	-	0.1(0.1)	P	-
Betula glandulosa	-	-	P	0.1 (0.1)	0.5 (0.1)
Shepherdia canadensis L.	-	-	P	0.5 (0.2)	2.8 (0.5)
Juniperus communis	-	-	P	P	0.2 (0.1)
Pinus albicaulis	-	-	-	0.1 (0.04)	0.3 (0.1)

Table 2-2. Continued

LAYER AND SPECIES	COMMUNITY TYPE				
	HEDYSARUM-SALIX	SALIX-DRYAS	DRYAS-HEDYSARUM	PICEA-SALIX	PICEA-ARCTOSTAPHYLOS
DWARF SHRUB LAYER					
Populus balsamifera	P	-	-	-	-
Salix ferrisae	0.2 (0.1)	-	-	-	-
Salix vestita	0.4 (0.2)	0.1 (0.1)	-	-	-
Salix myrtillifolia var. *cordata*	P	P	-	-	-
Salix brachycarpa ssp. brachycarpa	0.1 (0.1)	P	-	-	-
Salix reticulata ssp. *nivalis* (Hook.) Love & Love & Kapoor	0.2 (0.1)	P	-	-	-
Salix glauca	0.3 (0.1)	P	P	-	-
Salix arctica	P	0.1 (0.1)	P	-	-
Salix alaxensis	0.2 (0.1)	-	-	P	-
Picea engelmannii	0.1 (0.1)	0.1 (0.02)	P	0.1 (0.03)	0.1 (0.03)
Abies lasiocarpa	P	P	0.1 (0.03)	0.1 (0.03)	0.1 (0.04)
Dryas drummondii Richards.	1.2 (0.3)	3.8 (1.0)	18.6 (2.4)	1.1 (0.5)	0.1 (0.03)
Dryas integrifolia M. Vahl.	0.8 (0.3)	2.0 (0.8)	1.1 (0.5)	0.9 (0.5)	1.6 (0.4)
Arctostaphylos uva-ursi (L.) Spreng.	-	0.1 (0.1)	1.1 (0.6)	0.1 (0.1)	0.2 (0.1)
Dryas octopetala L.	-	1.5 (0.6)	0.4 (0.2)	0.8 (0.3)	2.4 (0.5)
Shepherdia canadensis	-	-	P	-	-
Juniperus communis	-	-	P	P	0.1 (0.04)
Arctostaphylos rubra (Rehder & Wils.) Fern.	-	-	1.3 (0.5)	9.4 (1.7)	12.8 (2.8)
Pinus albicaulis	-	-	-	P	0.1 (0.03)
GRAMINOID LAYER					
Poa alpina L.	P	P	0.1 (0.1)	P	P
Festuca saximontana Rydb.	-	P	-	-	-
Trisetum spicatum (L.) Richt.	-	-	P	P	P
Agropyron violaceum (Hornem.) Lange	-	-	0.1 (0.1)	0.1 (0.03)	0.1 (0.03)
Carex atrosquama Mack.	-	-	P	-	P
Carex aurea Nutt.	-	-	P	-	P
Carex concinna R. Br.	-	-	P	P	0.2 (0.04)
Carex scirpoidea Michx.	-	-	-	0.1 (0.03)	0.3 (0.1)
Agropyron trachycaulum (Link) Malte	-	-	-	-	P

Table 2-2. Continued

LAYER AND SPECIES	COMMUNITY TYPE				
	HEDYSARUM-SALIX	SALIX-DRYAS	DRYAS-HEDYSARUM	PICEA-SALIX	PICEA-ARCTOSTAPHYLOS
HERB LAYER					
Silene acaulis L.	P	-	-	-	-
Aster sp.	P	-	-	-	P
Saxifrage aizoides L.	P	P	-	-	-
Equisetum sp.	P	P	P	-	P
Corallorhize trifide Chatelain	P	0.1 (0.02)	-	P	-
Hedysarum boreale Nutt. var. *mackenzii* Rich.	5.2 (0.6)	7.0 (2.1)	17.8 (1.9)	12.9 (1.2)	3.5 (0.7)
Castilleia occidentalis Torr.	0.2 (0.04)	1.6 (0.4)	0.4 (0.1)	0.4 (0.2)	0.1 (0.1)
Saxifrage oppositifolia L.	-	P	-	-	-
Polygonum viviparum L.	-	P	-	-	-
Taraxacum officinale Weber	-	P	P	P	-
Pyrola asarifolia Michx.	-	P	0.2 (0.2)	0.1 (0.04)	0.6 (0.1)
Breya humilus (C.A. Mey) Robins	-	P	-	-	P
Epilobium anagallidifolium Lam.	-	-	P	-	-
Erigeron peregrinus (Pursh) Greene	-	-	P	-	-
Anemone parviflora Michx.	-	-	P	-	P
Epilobium angustifolium L.	-	-	P	0.1 (0.04)	P
Fragaria virginiana Duchesne	-	-	0.2 (0.1)	0.1 (0.1)	0.1 (0.04)
Solidago multiradiata Ait.	-	-	0.1 (0.1)	0.1 (0.04)	0.3 (0.1)
Habenaria viridis (L.) R. Br.	-	-	-	P	P
Pinguicula vulgaris L.	-	-	-	P	P
Moneses uniflora (L.) A. Gray	-	-	-	P	P
Pedicularis bracteosa Benth.	-	-	-	P	0.4 (0.2)
Antennaria rosea Greene	-	-	-	P	P
Antennaria lanata (Hook.) Greene	-	-	-	-	P
Antennaria neglecta Greene	-	-	-	-	P
Orthilia secunda (L.) House	-	-	-	-	P
Arnica cordifolia Hook.	-	-	-	-	P
Listera borealis Morong	-	-	-	-	P

Table 2-2. Continued

LAYER AND SPECIES	COMMUNITY TYPE				
	HEDYSARUM-SALIX	SALIX-DRYAS	DRYAS-HEDYSARUM	PICEA-SALIX	PICEA-ARCTOSTAPHYLOS
BRYOPHYTE LAYER					
Brachythecium sp.	P	3.5 (1.5)	3.6 (1.2)	10.6 (2.3)	4.3 (1.2)
Tortella inclinata (Hedw.) Limpr.	0.2 (0.1)	0.7 (0.3)	0.6 (0.3)	2.4 (0.8)	2.9 (0.5)
Ditrichum flexicaule (Schwaegr.) Hampe	0.1 (0.03)	0.9 (0.2)	1.6 (0.5)	5.3 (1.2)	2.6 (0.8)
Bryum sp.	0.6 (0.4)	2.5 (1.0)	2.0 (0.8)	5.9 (1.4)	2.2 (0.7)
Campylium sp.	0.1 (0.1)	0.6 (0.6)	0.1 (0.04)	1.3 (0.6)	0.6 (0.2)
Grimmia rivularis Brid.	-	0.2 (0.1)	0.1 (0.04)	0.2 (0.1)	0.5 (0.1)
Tortula norvegica (Web.) Wahlenb. ex Lindb.	-	P	0.2 (0.2)	1.0 (0.6)	1.1 (0.5)
Lescurea radicosa (Mitt.) Monk.	-	-	0.1 (0.1)	-	-
Thuidium abietinum (Hedw.) Warnst.	-	-	P	-	-
Hypnum revolutum (Mitt.) Lindb.	-	-	1.6 (1.0)	0.6 (0.3)	0.2 (0.1)
Rhacomitrichum canescens (Hedw.) Lindb.	-	-	-	P	P
Drepanocladus uncinatus (Hedw.) Warnst.	-	-	-	0.6 (0.5)	3.0 (1.4)
Barbilophozia lycopodioides (Wallr.) Loesk.	-	-	-	0.4 (0.4)	0.6 (0.3)
Ptilium crista-castrensis (Hedw.) De Not.	-	-	-	-	P
Hylocomium splendens (Hedw.) B.S.G.	-	-	-	-	0.3 (0.2)
Dicranum scoparium Hedw.	-	-	-	-	0.1 (0.1)
Lophozia sp.	-	-	-	-	0.6 (0.6)

Table 2-2. Concluded

LAYER AND SPECIES	COMMUNITY TYPE				
	HEDYSARUM-SALIX	SALIX-DRYAS	DRYAS-HEDYSARUM	PICEA-SALIX	PICEA-ARCTOSTAPHYLOS
LICHEN LAYER					
Peltigera rufescens (Weis) Humb.	P	-	0.1 (0.04)	0.7 (0.3)	0.2 (0.1)
Rinodina turfacea (Wahlenb.) Korber	-	0.4 (0.2)	P	P	0.6 (0.4)
Caloplaca sp.	-	P	-	0.1 (0.04)	0.4 (0.1)
Pannaria pezizoides (Weber) Trevisan	-	-	P	-	-
Cladonia chlorophaea (Florke ex Sommerf.) Sprengel	-	-	0.1 (0.1)	-	-
Cladonia pocillum (Ach.) O. Rich	-	-	-	0.3 (0.3)	-
Cladonia cariosa (Ach.) Spreng.	-	-	-	0.5 (0.03)	4.0 (1.2)
Cladonia pyxidata (L.) Hoffm.	-	-	-	0.5 (0.3)	3.6 (0.8)
Cetraria sp.	-	-	-	P	1.0 (0.7)
Buellia cf papillata (Sommerf.) Tuck	-	-	-	P	0.1 (0.03)
Peltigera aphthosa (L.) Willd.	-	-	-	-	P
Solorina sp.	-	-	-	-	P
Cladina mitis (Sandst.) Hustich	-	-	-	-	P
Dactylina ramulosa (Hook.) Tuck	-	-	-	-	0.3 (0.3)
OTHER					
Bare rock	83.8 (9.0)	29.5 (11.1)	22.4 (7.2)	7.8 (1.9)	2.6 (0.6)
Bare soil	14.2 (9.2)	4.4 (2.4)	6.6 (1.6)	0.6 (0.5)	0.7 (0.5)
Litter	0.5 (0.0)	46.7 (9.0)	52.4 (7.5)	62.1 (3.8)	71.9 (2.9)

Table 2-3. Species richness and mean cover (± standard error) within six vegetation layers from five successional community types on the Robson moraines. Species richness, diversity, evenness, dominance and species structure slope angle are shown for total vegetation cover (all layers).

	COMMUNITY TYPE				
	HEDYSARUM-SALIX (n=6)	SALIX-DRYAS (n=7)	DRYAS-HEDYSARUM (n=17)	PICEA-SALIX (n=20)	PICEA-ARCTOSTAPHYLOS (n=21)
SPECIES RICHNESS(S)					
Tree Layer	0	0	0	1	3
Shrub Layer	11	16	16	15	12
Dwarf Shrub Layer	13	11	11	10	10
Herb Layer	8	16	16	18	28
Bryophyte Layer	5	7	10	11	15
Lichen Layer	1	2	3	9	11
All Layers	26	37	49	57	70
MEAN COVER (%)					
Tree Layer	0	0	0	1.8 (0.8)	11.7 (1.3)
Shrub Layer	2.3 (1.0)	19.4 (1.6)	12.9 (1.7)	28.6 (1.6)	15.7 (1.3)
Dwarf Shrub Layer	3.2 (0.4)	7.4 (1.4)	21.5 (2.4)	12.1 (1.8)	17.1 (1.3)
Herb Layer	4.8 (0.6)	8.9 (2.3)	18.7 (1.9)	14.3 (1.1)	5.4 (0.7)
Bryophyte Layer	0.9 (0.2)	8.0 (2.0)	9.9 (2.0)	28.3 (3.0)	18.4 (2.3)
Lichen Layer	0.2 (0.1)	0.6 (0.3)	0.2 (0.1)	1.6 (0.5)	9.4 (1.4)
DIVERSITY (H')	2.28	2.66	2.29	2.71	3.05
EVENNESS (J')	0.701	0.737	0.589	0.669	0.719
DOMINANCE (C)	0.194	0.092	0.176	0.098	0.079
SLOPE ANGLE (A)	4.86	5.05	3.34	3.17	2.66

Table 2-4.. Total basal area (± standard error) of Picea engelmanii with a dbh>5 and mean stem density (± standard error) of Picea engelmannii from five successional community types on the Robson moraines. Mean density is partitioned into tree, shrub, and dwarf shrub layers.

	COMMUNITY TYPE				
	HEDYSARUM-SALIX (n=6)	SALIX-DRYAS (n=7)	DRYAS-HEDYSARUM (n=17)	PICEA-SALIX (n=20)	PICEA-ARCTOSTAPHYLOS (n=21)
Total Basal Area (m^2 ha^{-1})	0	0	0	2.9 (0.8)	15.0 (2.0)
Mean Density (# ha^{-1})	3400 (928)	4628 (736)	2259 (419)	5202 (825)	3569 (1073)
Tree Layer (%)	0	0	0	1.2	14.1
Shrub Layer (%)	11.8	47.8	68.8	81.5	21.9
Dwarf Shrub Layer (%)	88.2	52.2	31.2	17.3	64.0

2.6 References

Anonymous. 1982a. Canadian Climate Normals 1951-1980, Temperature. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 306 pp.

Anonymous. 1982b. Canadian Climate Normals 1951-1980, Precipitation. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 602 pp.

Birks, H.J.B. 1980. The present flora and vegetation of the moraines of the Klutlan Glacier, Yukon Territory, Canada: A study in plant succession. Quarternary Research 14: 60-86.

Coleman, A.P. 1910. Geology and glacial features of Mt. Robson. Can. Alpine J. 2: 108-113.

Cooper, W.S. 1916. Plant successions in the Mount Robson region, British Columbia. Plant World 19: 211-238.

Cooper, W.S. 1923. The recent ecological history of Glacier Bay, Alaska. Ecology 4: 223-246.

Cowles, H.C. 1899. The ecological relations of the vegetation on the sand dunes of Lake Michigan. Bot. Gaz. 27: 95-117.

Crocker, R.L. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecology 43: 428-448.

Dickson, B.A. and R.L. Crocker. 1953. A chronosequence of soils and vegetation near Mount Shasta, California. II. The development of

the forest floors and the carbon and nitrogen profiles of the soils. J. Soil Sci. 4: 142-154.

Egan, R.S. 1987. A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. The Bryologist 90: 77-173.

Eggler, W.A. 1941. Primary succession on volcanic deposits in Southern Idaho. Ecol. Monogr. 11: 278-298.

Fitter, A.H. and W.F.J. Parsons. 1987. Changes in phosphorus and nitrogen availability on recessional moraines of the Athabasca Glacier, Alberta. Can. J. Bot. 65: 210-213.

Field, W.O. and C.J. Heusser. 1954. Glacial and botanical studies in the Canadian Rockies, 1953. Can. Alpine J. 37: 127-140.

Gauch, H.G. 1982. Multivariate Analysis in Community Ecology. Cambridge University Press, New York, N.Y. 298 pp.

Giller, P.S. 1984. Community Structure and the Niche. Chapman and Hall, New York, N.Y. 176 pp.

Grime, J.P. 1979. Plant Strategies and Vegetation Processes. John Wiley and Sons, Toronto, Ont. 222 pp.

Heath, J.P. 1967. Primary conifer succession, Lassen Volcanic National Park. Ecology 48: 270-275.

Heusser, C.J. 1956. Post-glacial environments in the Canadian Rocky Mountains. Ecol. Monogr. 26: 263-302.

Hill, M.O. 1979. Twinspan - A Fortran Program for Arranging Multivariate Data in an Ordered Two-Way Table by Classification of the Individuals and Attributes. Cornell University, Ithaca, N.Y.

Holland, W.D. and G.M. Coen. 1983. Ecological (Biophysical) Land Classification of Banff and Jasper National Parks. Volume 1: Summary. Alberta Institute of Pedology, Edmonton, Alberta. Publ. No. M-83-2.

Huston, M. 1979. A general hypothesis of species diversity. Amer. Nat. 113: 81-101.

Ireland, R.R., C.D. Bird, G.R. Brassard, W.B. Schofield and D.H. Vitt. 1980. Checklist of the mosses of Canada. Publications in Botany, No. 8. Ottawa, Ont. 75 pp.

Kinney, G.B. 1909. Mount Robson. Can. Alpine J. 2: 1-9.

Lawrence, D.B. 1958. Glaciers and vegetation in south-eastern Alaska. Amer. Sci. 46: 89-122.

Leisman, G.A. 1957. A vegetation and soil chronosequence on the Mesabi iron range spoil banks, Minnesota. Ecol. Monogr. 27: 221-245.

Loucks, O.L. 1970. Evolution of diversity, efficiency and community stability. Amer. Zool. 10: 17-25.

Luckman, B.H. 1986. Reconstruction of Little Ice Age events in the Canadian Rocky Mountains. Geographie physique et Quaternaire 40: 17-28.

Margalef, D.R. 1958. Information theory in ecology. Gen. Syst. 3: 36-71.

Morrison, R.G. and G.A. Yarranton. 1974. Vegetational heterogeneity during a primary sand dune succession. Can. J. Bot. 52: 397-410.

Moss, E.H. 1983. Flora of Alberta. 2nd ed. (revised by J.G. Packer). University of Toronto Press, Toronto, Ont. 687 pp.

Mueller-Dombois, D. and H. Ellenberg. 1974. Aims and Methods of Vegetation Ecology. John Wiley and Sons, New York, N.Y. 547 pp.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Olson, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Bot. Gaz. 119: 125-170.

Pielou, E.C. 1974. Population and Community Ecology Principles and Methods. Gordon and Breach Sci. Publ., New York, N.Y. 424 pp.

Pielou, E.C. 1975. Ecological Diversity. John Wiley and Sons, Toronto, Ont. 165 pp.

Pielou, E.C. 1984. The Interpretation of Ecological Data. A primer on classification and ordination. John Wiley and Sons, Toronto, Ont. 263 pp.

Purchase, J.E. and G.H. La Roi. 1983. Pinus banksiana forests of the Fort Vermilion area, northern Alberta. Can. J. Bot. 61: 804-824.

Reiners, W.A., I.A. Worley and D.B. Lawrence. 1971. Plant diversity

in a chronosequence at Glacier Bay, Alaska. Ecology 52: 55-69.

Russell, W.B. and G.H. La Roi. 1986. Natural vegetation and ecology of abandoned coal-mined land, Rocky Mountain Foothills, Alberta, Canada. Can. J. Bot. 64: 1286-1298.

Shannon, C.E. and W. Weaver. 1949. The Mathematical Theory of Communication. University of Illinois Press, Urbana, Illinois.

Shure, D.J. and H.L. Ragsdale. 1977. Patterns of primary succession on granite outcrop surfaces. Ecology 58: 993-1006.

Simpson, E.H. 1949. Measurements of diversity. Nature (London) 163: 688.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd edition, W.H. Freeman & Co., San Francisco, California. 859 pp.

Sondheim, M.W. and J.T. Standish. 1983. Numerical analysis of a chronosequence including an assessment of variability. Can. J. Soil Sci. 63: 501-517.

Svoboda, J. and G.H.R. Henry. 1987. Succession in marginal Arctic environments. Arctic and Alpine Res. 19: 373-384.

Tisdale, E.W., M.A. Fosberg and C.E. Poulton. 1966. Vegetation and soil development on a recently glaciated area near Mount Robson, British Columbia. Ecology 47: 517-523.

Viereck, L.A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. Ecol. Monogr. 36: 181-199.

Viereck, L.A. 1970. Forest succession and soil development adjacent to the Chena river in interior Alaska. Arctic and Alpine Res. 2: 1-26.

Walker, L.R., J.C. Zasada and F.S. Chapin, III. 1986. The role of life history processes in primary succession on an Alaskan floodplain. Ecology 67: 1243-1253.

Wheeler, A.O. 1923. Motion of the Robson Glacier. Can. Alpine J. 13: 158-159.

Wheeler, A.O. 1932. Glacial changes in the Canadian Cordillera: The 1931 Expedition. Can. Alpine J. 20: 120-142.

Whittaker, R.H. 1972. Evolution and measurement of species diversity. Taxon 21: 213-251.

3. INTERSPECIFIC ASSOCIATIONS DURING PLANT SUCCESSION ON THE ROBSON MORAINES

3.1 Introduction

"Phytosociological structure" refers to the network of interspecific associations in a plant community resulting from the biological factors that cause different species of plants to grow close together or far apart (Dale 1982).

The non-random distribution or spatial pattern of plants in an early successional community can be partly the result of either positive or negative associations between species. Pattern may result when species develop competitive combining abilities (Aarssen 1983 c.f. ecological combining abilities (Harper 1977, p 268)). These competitive combining abilities can occur through reciprocal natural selection for traits which favour association. Other factors that cause pattern are competition for limited resources, differences in growth form, niche partitioning, heterogeneity in the environment, historical causes (e.g., seed bank), the combination of species that are available for establishment, differences in seed dispersal, animals, or disturbance (Greig-Smith 1979).

Morrison and Yarranton (1974) found that the number of interspecific associations increased with community development during the first 400 years of primary sand dune succession. Kershaw (1959), however, found that the number of associations between species decreased with increasing grassland community age. Similarily Aarssen and Turkington (1985) examined a chronosequence of pastures and found

that the frequency of random associations was higher in older pastures than in younger pastures. A similar trend was reported by O'Connor and Aarssen (1987) for species association patterns in a series of different-aged abandoned sand quarries.

The objective of this study was to examine interspecific associations on the 200 year old chronosequence of the Robson moraines and assess trends in this aspect of community development.

3.2 Site Description

Mount Robson (3954 m) is the tallest mountain in the Canadian Rockies and supports a major ice and snow field. The Robson Glacier, the largest on Mount Robson, has deposited a terminal moraine and approximately 10 recessional moraines during the past 200 years (Plate 2-1). The Robson moraines (53.1 °N, 119.1 °W) are situated at an elevation of 1662 ± 14 m. The moraines under study are 1.49, 1.38, 1.32, 1.17, 0.98, and 0.66 km north (315°) from the terminus of the glacier, and are referred to as moraines 1, 3, 4, 5, 7, and 8 (Heusser 1956), respectively. The moraines were formed in approximately 1801, 1891, 1907, 1912, 1933 and 1939.

No climatic data are available for the immediate area of Mount Robson. The nearest weather station is at Red Pass Junction, 20.2 km to the southeast of the mountain at an elevation of 1059 m. Mean daily temperature and total precipitation at this station are 1.7 °C and 742.6 mm. Approximately 54% of the total precipitation occurs as snowfall (Anonymous 1982a and b). The climate at the study site is undoubtedly colder and wetter than Red Pass Junction due to greater elevation. The 1985 mean daily air temperature and total precipitation for July and August were 11.1 °C and 16.3 mm and 7.5 °C

and 86.1 mm, respectively. The 1986 mean daily air temperature and total precipitation for July were 7.4 °C and 75.5 mm, and for August 1-23 were 9.3 °C and 10.5 mm, respectively (see Chapter 6).

Soil development in the study area was first described by Tisdale et al. (1966) and more recently by Sondheim and Standish (1983). In general, the soils are well drained loams with 40-70% coarse fragment (>2 mm) content. Orthic Regosols occur on the more recently formed moraines while Orthic Eutric Brunisols have developed on moraine 1. All soils are highly calcareous (76-86% $CaCO_3$ equivalent) and slightly alkaline (pH 7.95 to 7.75). On the oldest recessional moraine both soil organic matter and soil nitrogen content are approximately 10 times greater than that on the youngest (Sondheim and Standish 1983).

The vegetation on these moraines was representative of three phases of plant community development found on this chronosequence (see Chapter 2). The pioneer Hedysarum phase occurred on moraine 11 and was dominated by the herb Hedysarum boreale var. mackenzii Nutt. (Rich.)*, the low shrubs (<1 m in height) Salix vestita Pursh and Salix glauca L. and the dwarf shrub (<0.1 m in height) Dryas drummondii Richards. The Dryas transition phase occurred on moraines 7 and 5 and was dominated by D. drummondii, H. boreale and the low shrub S. glauca. Picea englmannii Parry ex Engelm. was beginning to emerge above the Salix on moraine 5. The oldest successional plant community (Picea phase) was found on recessional moraines 3, 2, and 1. It was dominated by P. engelmannii, the dwarf shrub Arctostaphylos rubra (Rehder & Wils.) Fern., H. boreale, the bryophyte genus

* Nomenclature follows Ireland et al. (1980), Moss (1983), and Egan (1987)

Brachythecium (species not differentiated), and the lichens Cladonia cariosa (Ach.) Spreng and C. pyxidata (L.) Hoffm.

3.3 Methods

Sampling

A plotless method of sampling vegetation was employed to detect interspecific associations (Yarranton 1966). Interspecific association analysis based on quadrat sampling is of limited value because the outcome of a test is dependent on the size of the quadrat selected (Pielou 1974). A plotless sampling method avoids the problem of sample scale and shape (Yarranton 1966).

Two hundred random point samples were recorded on each of moraines 8, 7, 5, 4, 3, and 1. At each point, the species hit by the sample point and the next different species in contact with it and nearest to the sample point, were recorded. In cases where a species hit by the sample point did not touch another plant, or where the only individuals contacted were members of the same species, a 'no contact' was recorded. 'No contact' samples were recorded to provide information on the tendency of a particular species to occur as isolated clumps or individuals.

Sampling was carried out in mid August 1986.

Statistical Analysis

The original data, including 'no contact' samples, were arranged in 2x2 contingency tables, and evidence of interspecific association was detected by the G-test of association applying William's correction (Sokal and Rohlf 1981). The traditional method of employing the 2x2 contingency table and chi-square statistic in the

analysis of plotless sampling data has been demonstrated to be incorrect (de Jong et al. 1980). As a consequence, the results of the traditional association analysis were used as an association index. This index was calculated based on joint presence or absence that resembles X^2 test calculations: $N(ad-bc)/(a+b)(a+c)(b+d)(c+d)$ where a pairs contained both species, d none, b and c contained one or other of the species but not both, and $N=a+b+c+d$ (cf. Pielou 1977, p. 207). Those pairs that gave an index value >4 were arbitrarily selected as indicating association and were used to examine trends in interspecific association on the moraines.

In order to test for evidence of significant interspecific associations, an iterative method of deriving maximum likelihood expected values for species-pair comparisons was used (de Jong et al. 1983). For the purpose of analysis, the data must be tabulated in an "unfolded" contingency table in which the order of contacts between species pairs are distinguished (de Jong et al. 1983, scheme (c)). 'No contact' samples were not treated as 'pseudospecies' and were not included in the association analysis. Evidence of non-randomness in the contingency table was detected by the G-test (Sokal and Rohlf 1981). The G-statistic was compared with a chi-square distribution with 1 degree of freedom. This test is a large sample test and is unreliable if the observed marginal totals are small. If there is an expected frequency less than 1 in any cell and/or expected frequencies less than 5 in more than 20% of its cells, the test cannot be legitimately applied (Zar 1984). Tables with cells with expected frequencies <1 and/or expected frequencies <5 in more than 20% of its cells were excluded from the analysis.

3.4 Results

The contingency matrix for each recessional moraine is presented in Appendix 3.

Association Index Method

On the early recessional moraine 8 both Dryas drummondii and Hedysarum boreale showed a propensity to occur as isolated clumps; 10 and 16% of the 200 sample random points hitting plants were recorded as 'no contact', respectively. This tendency to occur as isolated clumps was exibited only on newly exposed surfaces, Salix barclayi Anderss. and Poa alpina L. also tended to occur as isolated clumps.

Positive and negative interspecific associations detected by the association index method are shown in Table 3-1. The number of positive and negative associations based on the association index method are shown in Table 3-2.

There was little change in the number of positive associations with increasing moraine age. The number of negative associations increased to a high of 10 on the intermediate recessional moraines 4 and 5 and declined to a low of zero on recessional moraine 1. The proportion of positive and negative associations with a X^2 index greater than four relative to the total number of possible associations increased to a high of 80% on recessional moraine 4 and declined to a low of 17% on recessional moraine 1.

A few general interspecific association trends were evident on the Robson moraines. Hedysarum boreale was always negatively associated with Dryas drummundii on the youngest moraine 8 and the intermediate moraines 7 and 5 (Table 3-1). On moraines 5, 4, and 3 H. boreale was always negatively associated with Picea engelmannii and always

positively associated with Tortula norvegica (Web.) Wahlenb. ex Lindb. (Table 3-1).

Maximum Likelihood Method

Only one significant association was detected on the moraines when the maximum likelihood method of analysis was employed. Hedysarum boreale was found to be significantly positively associated with D. drummondii on the early recessional moraine 8 (G = 41.780). However, one association out of 27 tested might arise by chance alone. All the pairwise comparisons had to be rejected because of the occurrence of low expected frequencies.

3.5 Discussion

A comparison of the results of the association index method and the maximum likelihood method of association analysis showed that Hedysarum boreale var. mackenzii and Dryas drummondii were negatively associated in the former analysis and positively in the latter. The association index method of analysis includes 'no contact' samples and thus takes into account the tendency of H. boreale and D. drummondii to occur as isolated clumps on moraine 8. The maximum likelihood method of association analysis does not include 'no contact' samples, and when H. boreale and D. drummondii are only considered when in contact with other species, they are most often found in contact with one another. This is one limitation of the maximum likelihood method, in contrast to the association index method, since the probability of detecting a significant association is conditional on the rejection of isolated individuals. The maximum likelihood method did not detect any other associations on the moraines. It is probable that the small

sample size combined with relatively weak species interactions resulted in the lack of detectable associations among species.

The association index method showed little evidence of the establishment of successful co-existence between species on the Robson moraines. The majority of associations were negative which suggests that there has been competition between species for limiting resourses, and further supports the earlier finding (see Chapter 2) that resource preemption plays an important role in structuring the communities throughout the 200 year chronosequence.

Table 3-1. Positive and negative associations, detected by the association index method (see text p 70),on the Robson moraines. Pairs of species that have X^2 index values >4 are shown. "Positive" and "negative" refer to the sign of (ad-bc). Neither the order of the pairs nor the order of the species in a pair has any importance.

Positive	Negative
Moraine 8	
	Hedysarum boreale: *Bryum* spp.
	H. boreale: *Castilleja occidentalis*
	H. boreale: *Equisetum* spp.
	H. boreale: *Dryas drummondii*
	Dryas drummondii: *Salix barclayi*
Moraine 7	
Brachythecium spp.: *Tortula norvegica*	*H. boreale*: *Salix vestita*
	H. boreale: *Ditrichum flexicaule*
	H. boreale: *D. drummondii*
	D. drummondii: *T. norvegica*
	Brachythecium spp.: *Salix barclayi*
Moraine 5	
H. boreale: *T. norvegica*	*H. boreale*: *P. engelmannii*
P. engelmannii: *S. glauca*	*H. boreale*: *S. glauca*.
	H. boreale: *D. drummondii*
	H. boreale: *S. ferriae*
	H. boreale: *S. barclayi*
	H. boreale: *Ditrichum flexicaule*
	D. drummondii: *S. glauca*
	D. drummondii: *S. barclayi*
	D. drummondii: *T. norvegica*
	D. drummondii: *P. engelmannii*

Table 3-1 (concluded).

Positive	Negative
Moraine 4	
H. boreale: *T. norvegica*	*H. boreale*: *P. engelmannii*
P. engelmannii: *S. barclayi*	*H. boreale*: *S. glauca*
	H. boreale: *Ditrichum flexicaule*
	H. boreale: *Bryum* spp.
	T. norvegica: *Bryum* spp.
	T. norvegica: *Brachythecium* spp.
	T. norvegica: *S. barclayi*
	Bryum spp.: *S. barclayi*
	D. drummondii: *T. norvegica*
	D. drummondii: *P. engelmannii*
Moraine 3	
H. boreale: *T. norvegica*	*H. boreale*: *P. engelmannii*
	H. boreale: *S. glauca*
	H. boreale: *Bryum* spp.
	T. norvegica: *Ditrichum flexicaule*
Moraine 1	
Cladonia spp.: *Ditrichum flexicaule*	

Table 3-2. Positive and negative associations, detected by the association index method, on the Robson moraines. "Positive" and "negative" refer to the sign of (ad-bc). The number of "Total Possible" associations refers to the number of interspecific associations that were detected, and the "Proportion" refers to the percentage of associations with a X^2 index >4.

	Recessional Moraine					
Association	8	7	5	4	3	1
Positive	Ø	1	2	2	1	1
Negative	5	5	1Ø	1Ø	4	Ø
Total	5	6	12	12	5	1
Total possible	1Ø	16	17	15	9	6
Proportion (%)	5Ø	38	71	8Ø	56	17

3.6 References

Aarssen, L.W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. Amer. Natur. 122: 707-731.

Aarssen, L.W. and R. Turkington. 1985. Vegetation dynamics and neighbourhood associations in pasture community evolution. J. Ecol. 73: 585-603.

Anonymous. 1982a. Canadian Climate Normals 1951-1980, Temperature. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 306 pp.

Anonymous. 1982b. Canadian Climate Normals 1951-1980, Precipitation. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 602 pp.

Dale, M.R.T. 1982. Phytosociological structure of seaweed communities and the invasion of Fucus serratus in Nova Scotia. Can. J. Bot. 60: 2652-2658.

de Jong, P., L.W. Aarssen and R. Turkington. 1980. The analysis of contact sampling data. Oecologia 45: 322-324.

de Jong, P., L.W. Aarssen and R. Turkington. 1983. The use of contact sampling in studies of association in vegetation. J. Ecol. 71: 545-559.

Egan, R.S. 1987. A fifth checklist of the lichen-forming,

lichenicolous and allied fungi of the continental United States and Canada. The Bryologist 90: 77-173.

Greig-Smith, P. 1979. Pattern in vegetation. J. Ecol. 67: 755-779.

Harper, J.L. 1977. Population biology of plants. Academic Press, London. 892 pp.

Heusser, C.J. 1956. Postglacial environments in the Canadian Rocky Mountains. Ecol. Monographs 26: 263-302.

Ireland, R.R., C.D. Bird, G.R. Brassard, W.B. Schofield and D.H. Vitt. 1980. Checklist of the mosses of Canada. Publications in Botany, No. 8. Ottawa, Ont. 75 pp.

Kershaw, K.A. 1959. An investigation of the structure of a grassland community. III. Discussion and conclusions. J. Ecol. 47: 44-53.

Morrison, R.G. and G.A. Yarranton. 1974. Vegetational heterogeneity during a primary sand dune succession. Can. J. Bot 52: 397-410.

Moss, E.H. 1983. Flora of Alberta. 2nd ed. (revised by J.G. Packer). University of Toronto Press, Toronto, Ont. 687 pp.

O'Connor, I. and L.W. Aarssen. 1987. Species association patterns in abandoned sand quarries. Vegetatio 73: 101-109.

Pielou, E.C. 1974. Population and Community Ecology: Principles and Methods. Gordon and Breach Science Publ., New York, N.Y. 424 pp.

Pielou, E.C. 1977. Mathematical Ecology. Wiley, New York. 385 pp.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd edition, W.H. Freeman & Co., San Franscisco, Cal. 859 pp.

Tisdale, E.W., M.A. Fosberg and C.E. Poulton. 1966. Vegetation and soil development on a recently glaciated area near Mount Robson, British Columbia. Ecology 47: 517-523.

Yarranton, G.A. 1966. A plotless method of sampling vegetation. J. Ecol. 54: 229-237.

Zar, J.H. 1984. Biostatistical Analysis. 2nd edition, Prentice-Hall Canada Inc., Toronto, Ont. 718 pp.

4. PLANT COMMUNITY DEVELOPMENT AND THE ROLE OF NUCLEATION ON THE ROBSON MORAINES

4.1 Introduction

Three models of succession have been proposed by Connell and Slatyer (1977). These are known as the facilitation, inhibition and tolerance models. Facilitation is the classic model developed by Clements (1916) and later by Egler (1954) as Relay Floristics and by Horn (1976) as Obligatory Succession, which emphasizes that early colonizers 'prepare the ground' for subsequent colonizers, thus facilitating species replacement. Inhibition is related to Gleason's (1926) individualistic view of plant communities and differs from facilitation in that early colonizers resist the invasion of competitors by outcompeting them for limited resources and thus maintaining their own populations. The tolerance model suggests that late colonizers will be able to tolerate lower levels of resources than earlier colonizers. Thus they can invade and grow to maturity in the presence of those that precede them and still eventually dominate. This model was first proposed by Egler (1954) as the Initial Floristic Composition model and later by Horn (1976) as the Competitive Hierarchy model. Grime's (1981) model of vegetation succession emphasizes stress tolerance as a major component of succession.

In the few experimental investigations that have examined models of succession, inhibition occurs most frequently in many communities (see Dean and Hurd 1980; Turner 1983; Walker and Chapin 1986a and b).

Facilitation should be most common in harsh environments such as during primary succession where recruitment could be restricted by limiting abiotic factors (Connell and Slatyer 1977; Turner 1983). Early colonizers could ameliorate such impoverished environments by providing 'safe sites' (Harper 1977, p 111) for germination and/or ameliorating a barren substrate by contributing nutrients for the growth of subsequent colonizers.

Aarssen and Turkington (1985) have shown that very specific grass-legume associations can develop in mixed pastures which are partially influenced by nitrogen enrichment from Trifolium repens and its symbiont Rhizobium. Aarssen et al. (1979) proposed that the legume was a major 'driving force' in directing community change. Intensive studies of the nutritional role of the tree lupin Lupinus arboreus in coastal sand dune forestry in New Zealand showed that the lupin contributed approximately one quarter of the nitrogen required for Pinus radiata growth (Sprent and Silvester 1973; Sprent 1973). Jefferies et al. (1981) found that nitrogen accumulated by a legume may become available to an associated species on nutrient deficient mine spoils. They found that the biomass of the companion grass Agrostis castellana sown with the legume Trifolium repens was 4.75 times that of the grass grown in monoculture.

The legume Hedysarum boreale var. mackenzii (Rich.) Nutt. is an important colonizer (see Chapter 2) and primary contributor of biological nitrogen (see Chapter 6) on the Robson moraines. The same species is also an important colonizer of the Klutlan moraines, Yukon Territory (61 °N, 141 °W) (Birks 1980). Hedysarum mackenzii (= H. boreale var. mackenzii) has been reported to appear associated with

other pioneer species on the Robson moraines (Tisdale et al. 1966; Sondheim and Standish 1983) and on gravel outwash of the Muldrow Glacier, Alaska (63.4 °N, 150.6 °W) where the moss Ditrichum flexicaule was observed growing within clumps of H. boreale var. mackenzii (Viereck 1966).

The relationships between species can be separated into broad categories based on the "symmetry" of the relationship. Symmetric relationships arise when two species have similar or different ecological requirements and are called ecological coincidence or ecological divergence respectively (c.f., Dale 1977a). Asymmetric relationships result from the unidirectional effect of one species on the environment of another. This effect is called "influence" and is probably important in the development of patterns of species associations (Turkington et al. 1977).

The term "nucleation", first applied by Yarranton and Morrison (1974) to succession in plant communities, refers here to the possibility that Hedysarum clumps form centres of establishment and nuclei for the subsequent growth of other colonizers. If this is so, Hedysarum prepares the way for subsequent colonization which would be evidence of facilitation.

The objective of this study was to test the hypothesis that the early colonizer Hedysarum boreale facilitates colonization and thereby hastens vegetational development on the Robson moraines.

4.2 Site Description

Mount Robson (3954 m) is the tallest mountain in the Canadian Rockies and supports a major ice and snow field. The Robson Glacier,

the largest on Mount Robson, has deposited a terminal moraine and approximately 10 recessional moraines during the past 200 years (Plate 2-1). The Robson moraines (53.1 °N, 119.1 °W) are situated at an elevation of 1662 ± 14 m. The moraines under study are 1.49, 1.38, 1.17, 0.98, and 0.66 km north (315°) from the terminus of the glacier, and are referred to as moraines 1, 3, 5, 7, and 8 (Heusser 1956), respectively. The moraines were formed in approximately 1801, 1891, 1912, 1933 and 1939.

No climatic data are available for the immediate area of Mount Robson. The nearest weather station is at Red Pass Junction, 20.2 km to the southeast of the mountain at an elevation of 1059 m. Mean daily temperature and total precipitation at this station are 1.7 °C and 742.6 mm. Approximately 54% of the total precipitation occurs as snowfall (Anonymous 1982a and b). The climate at the study site is undoubtedly colder and wetter than Red Pass Junction due to greater elevation. The 1985 mean daily air temperature and total precipitation for July and August were 11.1 °C and 16.3 mm and 7.5 °C and 86.1 mm, respectively. The 1986 mean daily air temperature and total precipitation for July were 7.4 °C and 75.5 mm, and for August 1-23 were 9.3 °C and 10.5 mm, respectively (see Chapter 6).

Soil development in the study area was first described by Tisdale et al. (1966) and more recently by Sondheim and Standish (1983). In general the soils are well drainded loams with 40-70% coarse fragment (>2 mm) content. Orthic Regosols occur on the more recently formed moraines while Orthic Eutric Brunisols have developed on moraine 1. All soils are highly calcareous (76-86% $CaCO_3$ equivalent) and slightly alkaline (pH 7.95 to 7.75). On the oldest recessional moraine both

soil organic matter and soil nitrogen content are approximately 10 times greater than they are on the youngest (Sondheim and Standish 1983).

The vegetation on these moraines was representative of three phases of plant community development found on this chronosequence. The pioneer Hedysarum phase occurred on moraine 8 and was dominated by the herb Hedysarum boreale var. mackenzii Nutt. (Rich.) *, the low shrubs (<1 m in height) Salix vestita Pursh and Salix glauca L. and the dwarf shrub (<0.1 m in height) Dryas drummondii Richards. The Dryas transition phase occurred on recessional moraines 7 and 5 was dominated by D. drummondii, H. boreale and the low shrub S. glauca. Picea englmannii Parry ex Engelm. was beginning to emerge above the Salix on moraine 5. The oldest successional plant community (Picea phase) was found on moraines 3, 2 and 1 and the terminal. It was dominated by Picea engelmannii, the dwarf shrub Arctostaphylos rubra (Rehder & Wils.) Fern., H. boreale, the bryophyte Brachythecium spp., and the lichens Cladonia cariosa (Ach.) Spreng and C. pyxidata (L) Hoffn.

4.3 Methods

Sampling

Hedysarum boreale is a major colonizer on the Robson moraines. It grows in concentric clumps and is thus ideal for a test of nucleation. The following method is a simplified version of the sampling method used by Dale (1977b) to examine the incidence of asymmetric relationships (influence) in a mixed-forest community. The test was

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* Nomenclature follows Ireland et al. (1980), Moss (1983), and Egan (1987)

carried out on each of recessional moraines 8, 7, 5, 3, and 1 by comparing the frequency of species found within 200 randomly placed quadrats centred on H. boreale (neighbourhoods of Hedysarum) to the frequency of species found in 200 randomly placed quadrats (neighbourhoods of random points). The quadrats were circular and their diameter was determined by the average diameter of 100 randomly selected Hedysarum plants for each moraine.

Sampling was carried out in early July, 1985.

Statistical Analysis

In order to test for nonrandom interspecific association, the data was arranged in 2 x 2 contingency tables and possible evidence of nucleation was detected by the G-test of association applying William's correction (Sokal and Rohlf 1981). The G-statistic was compared with a chi-square distribution with 1 degree of freedom. This is a large sample test and is unreliable if the observed marginal totals are small. If an association table has an expected frequency <1 in any cell and/or expected frequencies < 5 in more than 20% of its cells, the test can not be legitimately applied (Zar 1984). Associations with cells with expected frequencies < 1 and/or expected frequencies < 5 in more than 20% of its cells were excluded from the analysis.

4.4 Results

The mean diameter in cm (± standard error) of 100 Hedysarum boreale clumps on each of moraines 8, 7, 5, 3, and 1 were 23.68 ± 1.37, 22.84 ± 0.83, 28.47 ± 1.23, 29.13 ± 1.61, and 14.95 ± 0.63,

respectively. The mean diameters of Hedysarum clumps were used to construct the circular quadrats. The results of the sampling and association analysis are shown in Tables 4-1 and 4-2 respectively.

On the youngest moraine 8, Dryas integrifolia L., the hemiparasite Castilleja occidentalis Torr., Salix glauca, and Salix seedlings were found significantly more often in the neighbourhood of H. boreale than in the neighbourhood of random points. On the next youngest moraine 7, Picea engelmannii and the moss Brachythecium spp. were found significantly more often in the neighbourhood of H. boreale than in the neighbourhood of random points; Dryas drummondii and D. octopetala L. were found in significantly fewer neighbourhoods of H. boreale than of random points. On the intermediate moraine 5, no positive associations were detected and only the moss Campylium spp. was found negatively associated with H. boreale centred quadrats. A similar situation was found on the older moraine 3, except that D. drummondii was found negatively associated with H. boreale. On the oldest recessional moraine 1, Pyrola asarifolia Michx., the mosses Brachythecium spp., Tortula norvegica (Web.) Wahlenb. ex Lindb. and Ditricum flexicaule (Schwaegr.) Hampe, and the lichen Cladonia spp. were found significantly more often in the neighbourhood of H. boreale than in the neighbourhood of random points; Dryas octopetala and D. integrifolia were found significantly less often in the nighbourhood of H. boreale than in the neighbourhood of random points.

4.5 Discussion

Nucleation within Hedysarum clumps occurs on the early recessional moraines 8 and 7 and the late recessional moraine 1. Most

importantly, on the youngest moraines, Salix glauca and Picea engelmannii are found associated (nucleated) with Hedysarum boreale var. mackenzii plants. These two species eventually become dominant species on the intermediate and late recessional moraines, respectively. On the oldest moraine (1), Brachythecium spp. and Cladonia spp. are dominant understory species and are found positively associated with H. boreale.

Nucleation occurs during the pioneer Hedysarum phase of community development when H. boreale patch size is increasing, and during the late Picea phase of community development when H. boreale patch size is decreasing (see Chapter 5). At this phase of succession Hedysarum may be preempting resourses and inhibiting colonization. During the intermediate phase of community development on moraines 5 and 3, Hedysarum patches are coalescing (see Chapter 5) and only significant negative associations with H. boreale are found (Table 4-2). During the early phase of community development, H. boreale clumps form centres of establishment for Salix seedlings and the subsequent growth of Salix glauca and Picea engelmannii. Hedysarum boreale may provide more hospitable sites for the germination of these species and eventual enrichment of the local substrate with nitrogen (through symbiotic Rhizobium) which could be used for the subsequent growth of these species. During the late phase of community development, H. boreale patches are breaking into smaller clumps and Brachythecium sp. and Cladonia sp. are occupying sites within and between these clumps.

Turner (1983) pointed out that in the few studies that have suggested that facilitation is the mechanism of community change, non-obligate facilitation is the most common. That is, late colonists can

establish in areas devoid of early colonists but establish faster in the presence of early colonists. Many of the colonizers which dominate the late phase of community development on the Robson moraines are also present in the early phase (see Chapter 2). If facilitation is occurring, it is probably non-obligate and may affect the rate of community development and not species composition on the Robson moraines. Hedysarum boreale is the primary contributor of biologically fixed nitrogen on the Robson moraines (see Chapter 6). Nitrogen enrichment from Hedysarum and its symbiont Rhizobium could become available to an associated species for subsequent growth and thus increase the rate of community development on the moraines.

The method of analysis used in this study provides correlative evidence of the role of nucleation in community development. Only an experimental approach will determine whether nucleation and thus facilitation is a mechanism of community development on the Robson moraines.

Table 4-1. The frequency of species found within 200 randomly placed quadrats and within 200 randomly placed Hedysarum boreale var. mackenzii quadrats (in brackets) in each moraine.

	RECESSIONAL MORAINE				
SPECIES	8	7	5	3	1
Dryas drummondii	60 (50)	82 (61)	98 (88)	34 (9)	2 (1)
D. octopetala	16 (27)	22 (9)	9 (12)	30 (21)	53 (27)
D. integrifolia	4 (14)	6 (8)	6 (3)	15 (10)	16 (6)
Arctostaphylos rubra	-	1 (1)	24 (20)	44 (42)	38 (28)
A. uva-ursi	-	1 (2)	4 (4)	5 (2)	-
Castilleja occidentalis	4 (34)	26 (34)	16 (18)	7 (6)	-
Saxifraga aizoides	12 (10)	0 (1)	-	-	-
Pyrola asarifolia	-	0 (1)	2 (3)	9 (6)	21 (43)
Antennaria rosea	1 (1)	-	-	1 (1)	0 (1)
Epilobium latifolium	3 (0)	2 (0)	0 (1)	-	-
E. angustifolium	-	-	3 (1)	8 (6)	-
Fragaria virginiana	-	-	7 (12)	25 (17)	2 (2)
Habenaria viridis	-	-	-	0 (1)	0 (1)
Corallorhiza trifida	2 (1)	-	-	1 (0)	-
Taraxacum officinale	-	-	0 (3)	-	-
Solidago multiradiata	-	-	-	3 (2)	2 (6)
Equisetum spp.	8 (7)	14 (14)	-	-	-
Carex scirpoidea	3 (0)	-	-	6 (2)	15 (7)
C. concinna	-	0 (1)	0 (1)	4 (2)	11 (13)
Agropyron violaceum	0 (1)	0 (1)	3 (6)	1 (0)	-
Poa alpina	15 (15)	8 (4)	6 (0)	1 (0)	-
Salix alaxensis	11 (19)	9 (11)	2 (0)	-	-
S. glauca	15 (31)	23 (12)	19 (19)	18 (27)	8 (5)
S. barclayi	16 (14)	19 (26)	18 (19)	6 (13)	3 (2)
S. vestita	14 (19)	7 (8)	11 (5)	3 (5)	3 (0)
S. reticulata ssp. nivalis	2 (8)	-	-	-	-

Table 4-1. Continued

SPECIES	RECESSIONAL MORAINE 8	7	5	3	1
Salix seedlings	3 (18)	-	-	-	-
Shepherdia canadensis	-	-	1 (1)	1 (3)	2 (2)
Betula glandulosa	-	-	-	-	3 (1)
Populus balsamifera	1 (2)	1 (0)	0 (1)	2 (0)	-
Abies lasiocarpa	0 (2)	2 (4)	0 (1)	-	1 (0)
Pinus albicaulis	-	-	-	1 (0)	-
Picea engelmannii	7 (11)	10 (21)	15 (22)	19 (23)	2 (2)
Brachythecium spp.	3 (5)	57 (85)	88 (87)	121 (110)	73 (117)
Bryum spp.	31 (29)	114 (121)	80 (76)	93 (78)	22 (35)
Tortula norvegica	2 (3)	39 (40)	26 (28)	18 (20)	9 (53)
Ditrichum flexicaule	28 (34)	68 (61)	45 (42)	105 (91)	84 (114)
Tortella inclinata	16 (19)	31 (34)	24 (27)	78 (70)	57 (61)
Campylium spp.	0 (1)	8 (5)	9 (1)	12 (19)	1 (3)
Drepanocladus uncinatus	1 (0)	3 (1)	7 (4)	6 (11)	12 (16)
Hypnum revolutum	0 (2)	0 (3)	6 (0)	-	1 (0)
Amblystegium varium	-	-	0 (2)	15 (19)	4 (9)
Hylocomium splendens	-	-	-	-	2 (0)
Cladonia spp.	-	2 (0)	-	30 (32)	73 (110)
Peltigera aphthosa	1 (2)	1 (0)	1 (0)	4 (6)	10 (11)
Alectoria sarmentosa	-	-	-	-	7 (10)
Dactylina ramulosa	-	-	-	-	1 (0)

Table 4-2. Species associations with Hedysarum boreale in each moraine detected by the G-test of association applying William's correction. Significant associations ($p < 0.05$) are underlined.

	RECESSIONAL MORAINE				
SPECIES	8	7	5	3	1
Dryas drummondii	- 1.249	-9.624	-1.001	-17.041	—
D. octopetala	+ 3.147	-5.985	+0.443	- 1.812	-57.920
D. integrifolia	+ 5.980	+0.290	-0.985	- 0.529	- 4.870
Arctostaphylos rubra	—	—	-0.404	- 0.059	- 1.806
Castilleja occidentalis	+25.590	+0.127	+0.128	- 0.077	—
Saxifraga aizoides	- 0.189	—	—	—	—
Pyrola asarifolia	—	—	—	- 0.607	+ 9.087
Epilobium angustifolium	—	—	—	- 0.287	—
Fragaria virginiana	—	—	+1.380	- 1.692	—
Equisetum spp.	- 0.067	—	—	—	—
Carex scirpoidea	- 3.584	—	—	—	- 3.076
C. concinna	—	—	—	—	+ 0.173
Poa alpina	—	-1.400	—	—	—
Salix alaxensis	+ 2.292	+0.207	—	—	—
S. glauca	+ 6.340	-3.795	—	+ 2.023	- 0.695
S. barclayi	- 0.142	+1.216	+0.029	+ 2.698	—
S. vestita	+ 0.310	+0.067	-2.326	—	—
S. reticulata ssp. nivalis	+ 3.762	—	—	—	—
Salix seedlings	+12.189	—	—	—	—
Picea engelmannii	+ 0.912	+4.251	+1.450	+ 0.421	—
Brachythecium spp.	—	+8.564	-0.010	- 1.235	+19.497
Bryum spp.	- 0.077	+0.508	-0.167	- 2.291	+ 3.449
Tortula norvegica	—	+0.016	+0.085	+ 0.114	+39.998
Ditrichum flexicaule	+ 0.684	-0.558	-0.131	- 1.955	+13.818
Tortella inclinata	+ 0.278	+0.164	-0.200	- 0.684	+ 0.191
Campylium spp.	—	-0.695	-7.166	+ 1.699	+ 0.942
Drepanocladus uncinatus	—	—	-0.815	+ 1.513	+ 0.605
Amblystegium varium	—	—	—	+ 0.507	+ 1.963
Cladonia spp.	—	—	—	+ 0.075	+13.820
Peltigera aphthosa	—	—	—	+ 0.393	+ 0.049
Alectoria sarmentosa	—	—	—	—	+ 0.540

4.6 References

Aarssen, L.W., R. Turkington and P.B. Cavers. 1979. Neighbour relationships in grass-legume communities. II. Temporal stability and community evolution. Can. J. Bot. 57: 2695-2703.

Aarssen, L.W. and R. Turkington. 1985. Biotic specialization between neighbouring genotypes in Lolium perenne and Trifolium repens from a permanent pasture. J. Ecol. 73: 605-614.

Anonymous. 1982a. Canadian Climate Normals 1951-1980. Temperature. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 306 pp.

Anonymous. 1982b. Canadian Climate Normals 1951-1980. Precipitation. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 602 pp.

Birks, H.J.B. 1980. The present flora and vegetation of the moraines of the Klutlan Glacier, Yukon Territory, Canada: a study in plant succession. Quaternary Res. 14: 60-86.

Clements, F.E. 1916. Plant Succession: An Analysis of the Development of Vegetation. Carnegie Inst. Publ. No. 242, Washington, D.C.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.

Dale, M.R.T. 1977a. Graph theoretical analysis of the phytosociological structure of plant communities: the theoretical

basis. Vegetatio 34: 137-154.

Dale, M.R.T. 1977b. Graph theoretical analysis of the phytosociological structure of plant communities: an application to mixed forest. Vegetatio 35: 35-46.

Dean, T.A. and L.E. Hurd. 1980. Development in an estuarine fouling community: the influence of early colonists on late arrivals. Oecologia 46: 295-301.

Egan, R.S. 1987. A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. The Bryologist 90: 77-173.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. Vegetatio 4: 412-417.

Gleason, H.A. 1926. The individualistic concept of the plant association. Bull. Torrey Bot. Club 53: 1-20.

Grime, J.P. 1981. Plant Strategies and Vegetation Processes. John Wiley & Sons, Toronto. 222 pp.

Harper, J.L. 1977. Population Biology of Plants. Academic Press, New York, N.Y. 892 pp.

Heusser, C.J. 1956. Post glacial environments in the Canadian Rocky Mountains. Ecol. Monographs 26: 263-302.

Horn, H.S. 1976. Succession. In: Theoretical Ecology: Principles and

Applications. Edited by R.M. May. Saunders, Philadelphia. pp 187-204.

Ireland, R.R., C.D. Bird, G.R. Brassard, W.B. Schofield and D.H. Vitt. 1980. Checklist of the mosses of Canada. Publications in Botany, No. 8. Ottawa, Ont. 75 pp.

Jefferies, R.A., A.D. Bradshaw and P.D. Putwain. 1981. Growth, nitrogen accumulation and nitrogen transfer by legume species established on mine spoils. J. Applied Ecol. 18: 945-956.

Moss, E.H. 1983. Flora of Alberta. 2nd ed. (revised by J.G. Packer). University of Toronto Press, Toronto, Ont. 687 pp.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd edition, W.H. Freeman & Co., San Franscisco. 859 pp.

Sondheim, M.W. and J.T. Standish. 1983. Numerical analysis of a chronosequence including an assessment of variability. Can. J. Soil Sci. 63: 501-517.

Sprent, J.I. and W.B. Silvester. 1973. Nitrogen fixation by Lupinus arboreus in the open and under different aged stands of Pinus radiata. New Phytol. 72: 991-1003.

Sprent, J.I. 1973. Growth and nitrogen fixation in Lupinus arboreus as affected by shading and water supply. New Phytol. 72: 1005-1022.

Tisdale, E.W. M.A. Fosberg and C.E. Poulton. 1966. Vegetation and soil development on a recently glaciated area near Mount Robson,

British Columbia. Ecology 47: 517-523.

Turkington, R.A., P.B. Cavers and L.W. Aarssen. 1977. Neighbour relationships in grass-legume communities. I. Interspecific contacts in four grassland communities near London, Ontario. Can. J. Bot. 55: 2701-2711.

Turner, T. 1983. Facilitation as a successional mechanism in a rocky intertidal community. Am. Nat. 121: 729-738.

Viereck, L.A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. Ecol. Monographs 36: 181-200.

Walker, L.R. and F.S. Chapin, III. 1986a. The role of life history processes in primary succession on an Alaskan floodplain. Ecology 67: 1243-1253.

Walker, L.R. and F.S. Chapin, III. 1986b. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecol. 67: 1508-1523.

Yarranton, G.A. and R.G. Morrison. 1974. Spatial dynamics of a primary succession: nucleation. J. Ecol. 62: 417-428.

Zar, J.H. 1984. Biostatistical Analysis. 2nd edition, Prentice-Hall Canada Inc., Toronto. pp 718.

PATTERN DEVELOPMENT OF SUCCESSIONAL PLANT COMMUNITIES ON THE ROBSON MORAINES

5.1 Introduction

The analysis of pattern (i.e., spatial dispersion of populations) employing data from transects of contiguous quadrats in plant communities is well documented (Greig-Smith 1979, 1983; Kershaw and Looney 1985). However, only a few studies have examined changes in species pattern during primary succession (e.g., Greig-Smith 1961b; Brereton 1971). The results of these and similar studies of secondary succession (e.g., Kershaw 1959, 1963) have shown that, in general, reductions in the number of scales of spatial pattern and in the intensity of patterns occur during the course of succession, which are indicative of community development approaching a steady state. Sondheim and Standish (1983) postulated that plant community development on the Mount Robson moraines," had reached a relatively stable seral state during which rates of change are comparitively slow."

The objectives of this study were: i) to examine the changes in the scale and intensity of spatial pattern of species occurring during plant community development on the Robson moraines; and ii) to test the hypothesis that spatial pattern development on the Robson moraines had reached a steady or stable state in 200 years.

5.2 Site Description

Mount Robson (3954 m) is the tallest mountain in the Canadian

Rockies and supports a major ice and snow field. The Robson Glacier, the largest on Mount Robson, has deposited a terminal moraine and approximately 10 recessional moraines during the past 200 years (Plate 2-1). The Robson moraines (53.1°N, 119.1°W) are situated at an elevation of 1662 ± 14 m. The moraines under study are 1.49, 1.38, 1.17, 0.98, and 0.66 km north (315°) from the terminus of the glacier. These recessional moraines were deposited in 1801, 1891, 1912, 1933, and 1939 and are referred to as moraines 1, 3, 5, 7, and 8, respectively (Heusser 1956).

The vegetation on these moraines is representative of three phases of plant community development found on this chronosequence. The first phase, the "pioneer" successional community, was dominated by Hedysarum boreale var. mackenzii Nutt. (Rich.)*, the low shrubs Salix vestita Pursh and Salix glauca L. (<1 m in height) and the dwarf shrub Dryas drummondii Richards. (<0.1 m in height). The second phase of successional plant community development found on moraines 7 and 5 were dominated by D. drummondii, H. boreale and the low shrub S. glauca. Picea englmannii Parry ex Engelm. was beginning to emerge above the Salix on moraine 5. The third phase, the oldest plant communities on the Robson moraines were found on moraines 3 and 1. They were dominated by P. engelmannii, the dwarf shrub Arctostaphylos rubra (Rehder & Wils.) Fern., H. boreale, the bryophyte Brachythecium sp., and the lichens Cladonia cariosa (Ach.) Spreng and C. pyxidata (L.) Hoffm.

No climatic data are available for the immediate area of Mount

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* Nomenclature follows Ireland et al. (1980), Moss (1983), and Egan (1987).

Robson. The nearest weather station is at Red Pass Junction, 20.2 km to the southeast of the mountain at an elevation of 1059 m. Mean daily temperature and total precipitation at this station are 1.7 °C and 742.6 mm. Approximately 54% of the total precipitation occurs as snowfall (Anonymous 1982a and b). The climate at the study site is undoubtedly colder and wetter than Red Pass Junction due to greater elevation. The 1985 mean daily air temperature and precipitation for July and August were 11.1 °C and 16.3 mm and 7.5 °C and 86.1 mm, respectively. The 1986 mean daily temperature and precipitation for July was 7.4 °C and 75.5 mm and for August 1-23 was 9.3 °C and 10.5 mm.

Soil development was first described by Tisdale et al. (1966) and more recently by Sondheim and Standish (1983). In general the soils are well drained loams with 40-70% coarse fragment (>2 mm) content. Orthic Regosols occur on the more recently formed moraines while Orthic Eutric Brunisols have developed on the older moraine 1. All soils are highly calcareous (76-86% $CaCO_3$ equivalent) and slightly alkaline (pH 7.95 to 7.75). On the oldest recessional moraine, both soil organic matter and soil nitrogen content are approximately 10 times greater than they are on the youngest (Sondheim and Standish 1983).

5.3 Methods

Field Studies

The percent cover of each species was estimated in 10x10 cm quadrats. This size was considered small enough to detect the pattern of most vascular plants and larger mats of mosses and lichen thalli,

but not so small that an impossibly large number of quadrats would be needed to cover a reasonable length of transect. A 30x30 cm frame was divided into a grid of 9 10x10 cm quadrats and sequentially placed along a 60 m belt transect. One belt transect of 1800 quadrats (3x600 quadrats) was sampled on each moraine. Each belt transect was randomly located within a 6 m section of the middle of the south slope of each moraine and traversed a predetermined survey line (see Figure 2-1).

Sampling was carried out during July and August 1985.

Pattern Analysis

The transect data were analyzed using Hill's (1973) two-term local quadrat variance (TTLQV) method, a modified block-size analysis of variance. Contiguous quadrats were sequentially blocked together in groups of 2, 3, 4 ... 150. The variance was plotted as a function of block size and peaks in this graph were interpreted as corresponding to the scales of pattern in the vegetation in the usual way (Greig-Smith 1961a; Usher 1975; Ludwig 1979; Kershaw and Looney 1985). The scale of pattern is defined by the average of the mean size of patches (dense vegetation) and the mean size of gaps (sparse vegetation) along the transect. Parallel transects of contiguous quadrats were employed to compare the peaks in variance and the heterogeneity among the variance-block size plots.

Recently Dale and MacIsaac (1988) have proposed refinements to the interpretation of Hill's (1973) TTLQV method. Their modifications enable one to estimate and compare the intensity of several peaks in the same data, to remove the overriding effect of larger more intense

patterns on less intense smaller scale patterns which are often obliterated or appear only as "shoulders" in the peaks associated with the larger block sizes (Figure 5-1), and to detect peaks that are due to resonance, i.e., harmonic or regular waves which occur in data with an exact periodicity (Usher 1975). For a perfect pattern, the intensity of pattern is essentially the difference between the mean abundance of vegetation in the patches and gaps. The estimated intensity $\underline{d}$ that gives rise to the peak in the variance-block size plot is defined by Dale and MacIsaac (1988) to be a function of the variance V_b at block size $\underline{b}$ and the block size:

$$d \equiv \sqrt{6b\, V_b/(b^2+2)}$$

where $\underline{d}$ is the intensity of a perfect patch at scale $\underline{b}$ that would give rise to the observed variance, the maximum possible would be around 100, since cover was measured as a percent.

Mean cover (% cover/10x10 cm quadrat) and the frequency (%) of each species in quadrats in each transect were included to aid in the interpretation of pattern intensity. A high proportion of empty quadrats can lead to aberrant results (Errington 1973; Ludwig and Goodall 1978) and caution should be exercised in interpreting the pattern results in such cases.

5.4 Results

The results of the pattern analysis for the most common species on the Robson Moraines are shown in Tables 5-1 to 5-13. In the tables the peaks are aligned in a totally subjective way to make comparisons easier. However, it is realized that this may give the impression

that there was more regularity among transects than there actually was. A summary of the number of scales of pattern for each species on each moraine are shown in Table 5-14. The raw data for each species in transect 2 are shown in Appendix IV.

There was little change in the number of scales of pattern with increasing surface age, and a general increase in the intensity of pattern of the dominant colonizer Hedysarum boreale with increasing surface age, reaching a maximum on the intermediate moraine 3 and declining on the oldest recessional moraine (Tables 5-1 and 5-14). Homogeneity among transects was highest on the early moraine 8 and at block sizes of 3 to 7 and 8 to 10 with increasing moraine age. Homogeneity refers to the coincident occurrence of three peaks at a particular block size range in the three transect analysis.

Dryas drummondii, a dominant colonizer on the intermediate moraines 7 and 5, showed little change in the number of scales of pattern with increasing surface age, and a general increase in pattern intensity with increasing surface age reaching a peak on moraine 5 (Tables 5-2 and 5-14). The scale of pattern was heterogeneous among the transects, as demonstrated by the occurrence usually of only 2 peaks at a particular block size in the three transect analysis (Table 5-2). Dryas octopetala L., a late colonizer on the Robson moraines, showed a general decline in the number of scales of pattern, and an increase in pattern intensity with increasing surface age (Tables 5-3 and 5-14).

Salix glauca, a dominant shrub on all the moraines showed a relatively stable number of scales of pattern with increasing moraine age, and an increase in pattern intensity with increasing surface age

reaching a peak on moraine 5 (Tables 5-4 and 5-14).

Salix vestita showed a persistent scale of pattern at a block size of 6 to 8 throughout the Robson chronosequence (Table 5-5). Pattern intensity and the number of scales of pattern declined with increasing moraine age (Table 5-14).

Salix barclayi (includes S. brachycarpa Nutt. ssp. brachycarpa which could not be readily distinquished from S. barclayi Anderss. in the field) showed several persistent scales of pattern on all the moraines (block sizes 6 to 8 and 16 to 21) (Table 5-6). Pattern intensity decreased with increasing surface age to a low on moraine 1. The number of scales of pattern showed little change with increasing moraine age (Table 5-14).

Arctostaphylos rubra, a dominant understory species on the older moraines (3 and 1), showed little change in the number of scales of pattern and pattern intensity with increasing surface age (Tables 5-7 and 5-14).

Picea engelmanii, the dominant species on the older recessional moraines, showed a general increase in pattern intensity with increasing surface age (Tables 5-8 and 5-14). The number of scales of pattern reached a peak on moraine 3 and declined slightly on moraine 1 (Table 5-14).

Cladonia spp., the dominant lichen on the oldest moraines (3 and 1), showed homogeneous scales of pattern among the three transects on moraine 7 (block size 3 to 4 and 19 to 22) and the older moraine 3 at block sizes of 4 to 6 and 33 to 36. Pattern intensity increased with surface age to a maximum on moraine 3 for several scales of pattern (block sizes 4 to 6 and 33 to 36), but continued to increase at block

sizes 11 to 14 (Table 5-9). The number of scales of pattern remained relatively constant with increasing moraine age (Table 5-14).

Brachythecium spp. (includes B. turgidum (C.J. Hartm.) Kindb. and B. groenlandicum (C. Jens.) Schljak.), the dominant moss on the moraines, showed a small increase in the number of scales of pattern and a general decline in pattern intensity with increasing surface age (Tables 5-10 and 5-14).

Bryum spp. generally showed a heterogeneous scale of pattern among the three transects on the moraines, except for block sizes 6 to 7 on moraine 3 and block sizes 22 to 25 on moraine 1 (Table 5-11). Pattern intensity generally increased with increasing surface age to a peak on the late recessional moraine 3. The number of scales of pattern increased with increasing moraine age (Table 5-14).

Tortella inclinata (Hedw.) Limpr. showed a decrease in the number of scales of pattern with increasing surface age, and an increase in pattern intensity with increasing moraine age to a maximum on moraine 3 (Table 5-14). On moraine 1 there was a minimal development of pattern with only a few single peaks in the variance-block size analysis (Table 5-12).

Ditrichum flexicaule (Schwaegr.) Hampe, also an important moss on the Robson moraines, generally showed heterogeneous scales of pattern among the three transects, except at a block size of 4 to 7 on moraines 8 and 5 and a block size of 11 to 14 on moraine 5 (Table 5-13). Changes in pattern intensity with age were generally irregular and lowest on moraine 5. The number of scales of pattern remained relatively constant on moraines 8 through 3 but declined on the oldest moraine (1) (Table 5-14). There was a minimal development of pattern

on moraine 1 even though the mean cover and frequency of occupied quadrats was highest on this moraine (Table 5-13).

5.5 Discussion

Kershaw (1959) and Greig-Smith (1961b) postulated that the initial colonization of an area would be random unless more favorable microsites were available to a species and then a non-random pattern could occur. In the early stages, pioneer species should show a relatively small scale of pattern, intense and morphologically determined, although environmental heterogeneity may result in a second larger scale of pattern. A maximum scale of pattern for any one species should be reached at the stage of succession optimal for the species. The later stages of succession should show either: a) a decrease in the scale of pattern if conditions for the species become unfavorable due to interference from other species, or b) an unchanged scale of pattern if conditions become generally unfavorable together with a decrease in intensity as a result of the random elimination of individuals within patches. The later stages of community development should show little pattern (the random distribution of individuals) with a reduction in the intensity and number of scales of pattern which are indicative of vegetation development approaching a steady state.

The results of the spatial pattern analysis by species of the Robson chronosequence showed that pattern intensity increased initially followed by a general reduction in the intensity of pattern with community development following the trends suggested by Greig-Smith (1961) and Kershaw (1959). However, the number of scales of

pattern by species remained relatively constant on the Robson chronosequence, and showed no tendency to decrease on the older moraines.

It is concluded that the changes in species spatial pattern that have occurred in the last 200 years on the Robson moraines do not represent an initial phase of vegetation change culminating in a steady state in community development. This conclusion is also supported by the absence of some species on the older moraines that are characteristic of old-growth forests in the area such as Cornus canadensis L. and Pleurozium schreberi (Brid.) Mitt. Abies lasiocarpa, a dominant old-growth forest species is still sporadic on the moraines (see Chapter 2). This is not consistent with the findings of Sondheim and Standish (1983), that nitrogen and organic carbon in soils on the Robson moraines appear to have reached a "temporary steady state" in less than 200 years, during which rates of change are relatively low.

Figure 5-1. Two-term local quadrat variance (TTLQV) plots for two scales of pattern (block size 4 and 22) with three intensities at the larger scale (from Dale and McIsaac 1988).

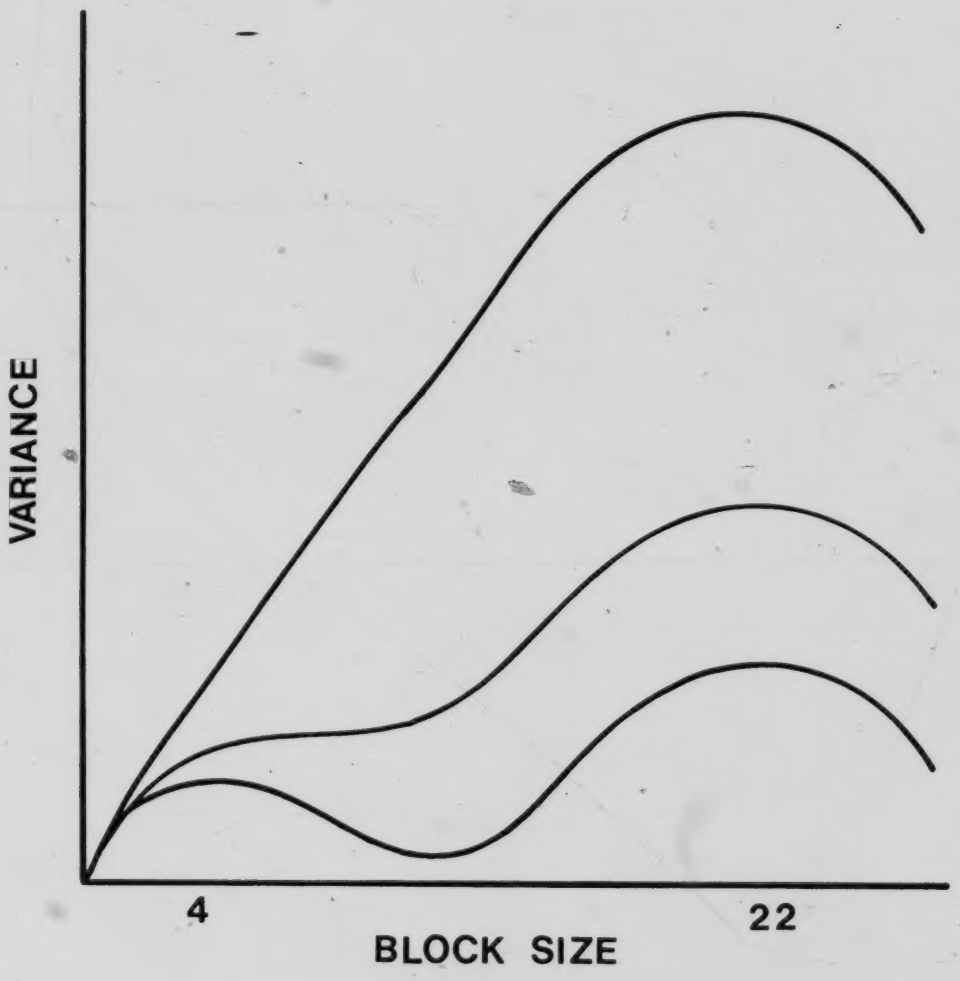
VARIANCE
4
22
BLOCK SIZE

Table 5-1. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Hedysarum boreale on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2 and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)					
8	1	1.92	20.33	4 (13.8)	8 (8.5)	12 (5.3)	18 (4.3)	31 (3.9)	50 (3.2)
	2	2.59	25.67	4 (16.3)	8 (3.6)	12 (9.3)	20 (6.8)	28 (5.3)	
	3	2.58	24.50	5 (14.6)	9 (10.7)	15 (6.9)	22 (6.8)		
7	1	5.20	57.67	5 (9.9)					
	2	5.47	56.50		9 (9.2)			30 (5.2)	
	3	4.88	53.67		10 (9.7)			33 (5.6)	
5	1	7.56	69.17		9 (9.2)	15 (5.2)	21 (4.2)	32 (2.6)	
	2	8.18	70.50		10 (9.0)		23 (6.7)		
	3	8.70	71.67	5 (14.5)	8 (9.4)	12 (7.3)	21 (4.5)	28 (2.4)	46 (6.4)
3	1	9.76	75.33	3 (15.6)	10 (12.1)	15 (5.8)			45 (7.6)
	2	11.25	75.17			13 (10.8)			45 (7.8)
	3	11.52	77.17	7 (12.5)				27 (10.4)	43 (6.4)
1	1	3.47	30.83	6 (9.2)			22 (5.7)	27 (5.1)	
	2	3.77	32.17	4 (11.5)		16 (6.7)			
	3	3.68	32.00	4 (12.0)	9 (6.0)				

Table 5-2. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Dryas drummondii on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)						
8	1	0.36	7.83		12 (2.9)					
	2	0.20	9.67	8 (1.2)	13 (0.8)		18 (0.6)	24 (.04)		
	3	0.24	10.17	6 (2.5)	10 (1.7)		18 (1.1)			
7	1	3.76	41.33	6 (9.1)	10 (5.7)	14 (5.0)	18 (4.3)	22 (4.2)		
	2	3.72	39.67	6 (9.3)	10 (5.7)	14 (4.9)	18 (3.9)	22 (4.0)		46 (2.0)
	3	4.19	42.67		9 (8.5)					
5	1	10.49	66.17				17 (10.5)			49 (8.7)
	2	9.95	65.00	8 (13.2)	12 (10.6)					44 (9.2)
	3	10.07	66.33		12 (11.5)					49 (2.4)
3	1	1.37	13.83	7 (5.0)			16 (5.1)		32 (4.0)	43 (2.3)
	2	1.31	14.17		12 (5.1)				35 (4.1)	
	3	1.44	15.83	4 (6.1)	10 (3.2)		19 (5.0)		38 (3.9)	

Table 5-3. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Dryas octopetala on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)									
7	1	0.33	3.83		12 (3.0)								
	2	0.31	2.83	4 (3.6)	12 (2.6)	19 (1.4)							
	3	0.52	3.17	6 (5.0)			24 (1.4)			38 (1.7)			
3	1	1.09	12.67		15 (3.8)		23 (3.1)						
	2	1.07	11.17	9 (4.7)				29 (3.6)					
	3	1.00	10.50	4 (5.7)			23 (3.9)			38 (2.6)			
1	1	5.77	42.33		12 (10.1)					36 (11.1)			
	2	5.15	42.17		13 (8.6)					38 (9.2)			
	3	5.03	40.50		14 (9.5)							45 (8.1)	

Table 5-4. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Salix glauca on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)					
8	1	0.47	4.33				18 (4.2)		
	2	0.44	4.33				18 (4.4)		
	3	0.58	5.00		8 (5.2)		21 (5.1)	32 (2.2)	
7	1	1.35	9.00	3 (11.3)		12 (8.3)	18 (3.8)		43 (3.9)
	2	1.45	9.33	3 (8.5)	8 (8.5)	13 (5.3)		35 (4.9)	
	3	1.52	6.67		7 (9.3)				38 (6.5)
5	1	2.17	12.17	5 (10.8)		14 (9.7)	23 (5.8)	32 (3.6)	
	2	2.29	10.00	5 (13.6)			20 (8.8)	32 (4.9)	
	3	1.34	7.50		10 (7.8)	16 (4.5)			
3	1	0.96	8.50	4 (5.8)		13 (4.6)	20 (2.3)	30 (0.9)	
	2	0.95	6.83	6 (8.3)			17 (5.2)		
	3	1.38	7.17	6 (9.1)			18 (6.5)	31 (4.8)	
1	1	1.06	3.50	4 (8.5)	10 (9.1)		17 (5.6)		38 (5.5)
	2	1.13	5.17	5 (5.7)	11 (7.9)		18 (4.8)		41 (4.3)
	3	0.26	2.33	3 (10.6)	9 (10.3)		15 (6.1)	33 (4.9)	39 (4.6)

Table 5-5. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Salix vestita on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)						
8	1	0.47	4.83		5 (4.0)	8 (2.6)	12 (1.8)	18 (1.2)	21 (2.6)	28 (0.5)
	2	0.51	3.17		5 (5.2)	8 (3.3)	11 (2.4)	18 (1.2)	24 (2.0)	28 (1.1)
	3	0.38	4.33	3 (4.9)	5 (2.4)	8 (3.8)	12 (1.1)	17 (2.1)		29 (1.2)
7	1	2.94	10.50	3 (17.4)		7 (17.5)	11 (8.9)		24 (6.4)	
	2	2.55	9.67		5 (12.5)		14 (8.9)		22 (1.9)	29 (8.9)
	3	2.99	9.17			8 (17.5)				29 (12.0)
5	1	1.91	4.50	3 (18.3)			12 (14.6)	20 (11.3)		31 (6.5)
	2	1.70	4.17			7 (13.0)		19 (13.4)		28 (6.1)
	3	0.90	4.17		5 (10.2)			18 (7.1)		27 (3.9)
3	1	0.53	2.67				12 (4.7)			
	2	0.39	1.83			8 (4.4)				
	3	0.61	3.67			6 (5.9)			22 (3.7)	
1	1	0.97	5.00			7 (6.9)		20 (6.4)		28 (5.4)
	2	1.11	5.50			6 (7.0)		19 (6.7)		29 (2.9)
	3	1.43	6.00	3 (5.7)		7 (11.3)		16 (3.5)		30 (7.4)

Table 5-6. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Salix barclayi on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)						
8	1	0.56	6.17		6 (4.5)		21 (3.1)		32 (1.7)	
	2	0.79	5.83		7 (6.6)			25 (4.2)		39 (2.1)
	3	0.48	6.83		8 (3.6)			26 (2.4)		40 (0.8)
7	1	3.15	16.83	5 (12.7)		13 (10.6)	21 (1.8)		28 (7.4)	
	2	3.06	17.17		8 (13.3)				32 (8.5)	
	3	2.99	14.00		7 (14.3)			24 (11.0)		36 (5.2)
5	1	1.52	7.67	3 (9.0)	7 (10.3)	12 (7.3)	17 (6.9)			40 (6.3)
	2	1.84	9.67		6 (11.0)			26 (7.4)		42 (5.0)
	3	2.15	10.67		6 (12.1)			25(8.6)		38 (4.6)
3	1	2.33	16.17	5 (12.8)	8 (6.6)	11 (3.3)	19 (7.3)		32 (5.0)	
	2	1.83	14.33	5 (9.7)			17 (7.2)	25(6.1)		38 (4.2)
	3	2.27	16.83		6 (8.8)		17 (7.3)	25 (8.6)		39 (4.0)
1	1	1.16	8.67	5 (6.4)			16 (4.7)		32 (3.4)	
	2	1.23	8.67	4 (8.9)		13 (6.1)	20 (3.2)		30 (1.8)	40 (3.1)
	3	1.06	8.00	3 (7.6)	8 (6.9)	13 (4.2)			29 (2.2)	

Table 5-7. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Arctostaphylos rubra on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)			
3	1	2.34	8.33		17 (9.3)	43 (11.8)	70 (7.5)
	2	2.31	9.67		18 (8.4)	44 (10.7)	69 (6.5)
	3	2.54	10.00		18 (9.9)	44 (12.0)	70 (7.5)
1	1	6.58	24.83	6 (17.6)	16 (11.4)	38 (16.7)	61 (9.7)
	2	4.85	22.67	12 (12.3)		37 (11.0)	60 (7.3)
	3	3.64	18.50	8 (13.3)	19 (11.4)	34 (8.4)	56 (5.4)

Table 5-8. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Picea engelmannii on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)								
7	1	3.31	7.00	6 (11.3)	15 (24.3)	22 (11.3)			52 (69.8)			
	2	3.71	7.17	7 (13.8)	16 (25.5)	22 (9.5)			53 (15.3)			
	3	3.70	8.00	7 (13.2)	16 (26.1)	22 (10.2)			57 (15.4)			
3	1	13.07	26.50	9 (31.0)		20 (14.4)	33 (17.6)	40 (30.7)	50 (19.3)			
	2	13.74	25.50	10 (35.2)		20 (48.0)	34 (11.2)	38 (33.1)	52 (19.8)			
	3	14.62	27.33	8 (30.0)		19 (51.1)	31 (33.4)	44 (25.0)				
1	1	20.42	24.50									
	2	20.53	26.17				29 (50.9)			60 (37.5)	149 (52.3)	
	3	21.04	28.50				29 (50.8)			56 (38.1)	146 (52.6)	

Table 5-9. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Cladonia sp. on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)					
7	1	0.25	11.00	4 (1.7)		14 (2.9)	20 (0.8)		
	2	0.23	10.17	4 (1.6)			19 (0.9)	29 (0.4)	
	3	0.19	10.83	3 (1.2)	7 (0.6)	11 (0.4)	22 (1.2)		37 (0.4)
5	1	0.14	19.33	6 (0.3)	9 (0.4)	14 (0.3)			
	2	0.20	21.17		7 (0.7)	12 (0.5)	16 (0.4)	30 (0.3)	
	3	0.17	19.50	4 (0.7)				31 (0.3)	
3	1	2.90	39.33	4 (12.1)			18 (9.3)		36 (7.5)
	2	2.90	36.17	6 (12.4)	10 (6.4)	14 (5.5)			34 (9.3)
	3	2.79	38.67	5 (8.5)		12 (6.3)			33 (9.2)
1	1	4.16	65.67		8 (8.3)		21 (6.7)	31 (5.3)	
	2	4.45	68.17	5 (7.5)		13 (8.0)	21 (5.0)	30 (3.5)	
	3	4.45	67.67			12 (6.6)			33 (5.4)

Table 5-10. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Brachythecium sp. on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)						
7	1	1.56	22.83	3 (15.9)		10 (9.9)		20 (7.3)		35 (4.5)
	2	1.14	24.33	3 (8.9)		8 (7.3)		19 (3.2)		
	3	1.05	25.50	3 (8.8)				19 (4.0)	28 (1.6)	
5	1	1.86	24.33		4 (12.2)		12 (10.6)		28 (3.6)	
	2	1.73	25.00		4 (12.5)	8 (10.6)	13 (8.7)	20 (1.6)		
	3	1.27	25.50						27 (7.6)	
3	1	2.21	54.83				12 (9.1)			34 (8.0)
	2	2.53	56.83			8 (8.0)		22 (8.7)		34 (3.9)
	3	1.21	50.83			9 (8.5)			26 (5.3)	39 (2.2)
1	1	0.93	44.83		5 (5.4)	8 (3.3)	12 (2.6)	18 (1.4)	26 (2.7)	
	2	0.77	45.33		4 (3.7)	7 (1.6)			25 (1.5)	
	3	0.91	45.67	3 (5.9)	5 (3.5)	7 (2.8)	11 (2.4)	23 (0.9)		37 (2.7)

Table 5-11. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Bryum sp. on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)							
8	1	0.30	10.83			13 (3.5)					
	2	0.44	11.83				18 (4.0)				
	3	0.37	10.00				16 (3.7)				
7	1	3.87	59.67			13 (8.8)			29 (5.6)		
	2	3.42	62.00				21 (5.8)				
	3	4.08	66.83		6 (11.1)		19 (7.2)				
5	1	1.47	36.17							36 (2.1)	
	2	1.38	40.50		6 (3.7)		20 (3.1)			34 (2.1)	37 (0.7)
	3	1.33	41.17	3 (6.9)			17 (3.9)		28 (2.7)		40 (2.2)
3	1	3.88	64.67		7 (8.0)		18 (10.0)		26 (2.6)		39 (6.4)
	2	4.02	61.33		6 (10.0)	9 (8.0)		23 (9.7)		36 (5.1)	
	3	3.72	63.17		7 (7.0)		19 (8.4)		30 (4.0)		39 (5.4)
1	1	0.30	20.67		5 (1.3)			23 (1.8)		36 (0.5)	
	2	0.33	19.33			9 (1.0)		22 (0.9)			
	3	0.41	19.33	3 (2.5)		11 (1.7)	18 (0.9)	25 (0.5)		34 (6.7)	

Table 5-12. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Tortella inclinata on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)						
7	1	0.64	13.83							25 (2.8)
	2	0.42	13.17							24 (1.8)
	3	0.40	11.50						19 (2.4)	25 (2.2)
5	1	0.31	12.00		5 (1.9)	8 (2.1)			22 (0.9)	
	2	0.60	18.00		4 (5.4)			13 (3.6)		25 (2.2)
	3	0.35	13.83	3 (2.8)	5 (1.3)		11 (1.4)		19 (1.0)	
3	1	6.80	53.00		4 (14.9)		10 (15.9)	16 (7.7)		
	2	5.65	53.00	3 (14.8)			9 (16.1)	14 (9.8)	20 (5.3)	
	3	4.64	52.33	3 (14.7)			10 (10.2)	16 (5.2)		
1	1	1.94	49.33			7 (3.9)			19 (3.4)	
	2	2.49	52.17					15 (5.0)		
	3	2.45	51.00							

Table 5-13. The scale (peaks in the variance-block size plots) and intensity (estimated difference in the abundance of vegetation in patches and gaps) of pattern of Ditrichum flexicaule on the Robson moraines. One unit of block size = 10 cm. (Mean cover = % cover/100 cm^2) and % frequency = percentage of quadrats occupied by the species)

Moraine	Transect	Mean Cover	% Frequency	Block Size (Intensity)					
8	1	0.41	10.67	6 (4.6)	10 (3.7)	16 (2.7)			
	2	0.32	10.83	7 (2.0)		18 (2.1)		31 (1.4)	
	3	0.28	13.50	4 (1.3)	12 (1.3)				
7	1	1.12	29.00					27 (4.3)	
	2	1.52	31.00	4 (8.4)	9 (4.6)				39 (3.8)
	3	1.63	33.67		12 (5.7)				
5	1	0.11	7.50	6 (0.6)	14 (0.5)		22 (0.4)		37 (0.3)
	2	0.18	7.33	6 (1.1)	12 (0.7)	17 (0.8)		30 (1.0)	38 (1.0)
	3	0.21	10.00	4 (1.4)	11 (0.9)	17 (0.6)	25 (0.5)		
3	1	2.54	44.33						38 (7.3)
	2	2.82	47.50		10 (7.9)	19 (5.7)			
	3	2.62	48.50	5 (9.3)					34 (7.4)
1	1	4.91	62.00			21 (7.8)			
	2	4.76	61.67						34 (5.9)
	3	4.48	60.00						37 (4.7)

Table 5-14. The number of scales of pattern (peaks in the variance-block size plots) for each species on the Robson moraines. For each species the moraine with the highest intensity of pattern is underlined.

Species	Moraine 8	7	5	3	1
Hedysarum boreale	6	3	6	5	5
Dryas drummondii	4	6	4	5	-
Dryas octopetala	-	5	-	5	3
Salix glauca	3	5	5	5	5
Salix vestita	7	6	6	3	4
Salix barclayi	5	7	6	7	6
Arctostaphylos rubra	-	-	-	3	4
Picea engelmannii	-	4	-	5	3
Cladonia spp.	-	6	5	5	6
Brachythecium spp.	-	5	5	5	7
Bryum	2	4	6	7	6
Tortella inclinata	-	2	7	5	3
Ditrichum flexicaule	4	4	6	4	2

5.6 References

Anonymous. 1982a. Canadian Climate Normals 1951-1980. Temperature. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 306 pp.

Anonymous. 1982b. Canadian Climate Normals 1951-1980. Precipitation. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 602 pp.

Brereton, A.J. 1971. The structure of the species populations in the initial stages of salt-march succession. J. Ecol. 59: 321-338.

Dale, M.R.T. and D.A. MacIsaac. 1988. New methods for the analysis of spatial pattern in vegetation. J. Ecol. (in press).

Egan, R.S. 1987. A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. The Bryologist 90: 77-173.

Errington, J.C. 1973. The effect of regular and random distributions on the analysis of pattern. J. Ecol. 61: 99-105.

Greig-Smith, P. 1961a. Data on pattern within plant communities. I. The analysis of pattern. J. Ecol. 49: 695-702.

Greig-Smith, P. 1961b. Data on pattern within plant communities. II. Ammophila arenaria (L.) Link. J. Ecol. 49:703-708.

Greig-Smith, P. 1979. Pattern in vegetation. J. Ecol. 67: 755-779.

Greig-Smith, P. 1983. Quantitative Plant Ecology. Third Edition.

Blackwell Scientific Publ., Boston, Mass. 347 pp.

Heusser, C.J. 1956. Post glacial environments in the Canadian Rocky Mountains. Ecol. Monographs 26: 263-302.

Hill, M.O. 1973. The intensity of spatial pattern in plant communities. J. Ecol. 61: 225-235.

Kershaw, K.A. 1959. An investigation of the structure of a grassland community. II. The pattern of Dactylis glomerata, Lolium perenne and Trifolium repens. III. Discussion and Conclusions. J. Ecol. 47: 31-53.

Kershaw, K.A. 1963. Pattern in vegetation and its causality. Ecology 44: 377-388.

Ireland, R.R., C.D. Bird, G.R. Brassard, W.B. Schofield and D.H. Vitt. 1980. Checklist of the mosses of Canada. Publications in Botany, No. 8. Ottawa, Ont. 75 pp.

Ludwig, J.A. and D.W. Goodall. 1978. A comparison of paired- with blocked-quadrat variance methods for the analysis of spatial pattern. Vegetatio 38: 49-59.

Ludwig, J.A. 1979. A test of different quadrat variance methods for the analysis of spatial pattern. In: Spatial and Temporal Analysis in Ecology. Edited by R.M. Cormack and J.K. Ord. International Co-operative Publ. House, Fairland, Maryland. pp 289-304.

Moss, E.H. 1983. Flora of Alberta. 2nd ed. (revised by J.G. Packer).

University of Toronto Press, Toronto, Ont. 687 pp.

Sondheim, M.W. and J.T. Standish. 1983. Numerical analysis of a chronosequence including an assessment of variability. Can. J. Soil Sci. 63: 501-517.

Usher, M.B. 1975. Analysis of pattern in real and artifical plant populations. J. Ecol. 63: 569-586.

6. DINITROGEN FIXATION (ACETYLENE REDUCTION) IN PRIMARY SUCCESSION NEAR MOUNT ROBSON, BRITISH COLUMBIA *

6.1 Introduction

All the nutrients required for plant growth are often present in the soil parent material, except nitrogen (Jenny 1980), which originates primarily through biological-fixation (Black 1968). Nitrogen is often limiting in the early stages of primary succession (Vitousek and Walker 1987) and is a critical factor in the development of ecosystems (Marrs et al. 1981).

The importance of nitrogen-fixing organisms in the build-up of soil nitrogen during primary succession has been widely reported (e.g., Dickson and Crocker 1954; Crocker and Major 1955; Crocker and Dickson 1957; Leisman 1957; Olson 1958; Tezuka 1961; Tisdale et al. 1966; Viereck 1966; Lawrence et al. 1967; Stewart and Pearson 1967; Syers et al. 1970; Van Cleve et al. 1971; Jacobson and Birks 1980; Skeffington and Bradshaw 1980; Fitter and Parsons 1986). However, only three of the aforementioned studies have examined biological dinitrogen fixation directly. Lawrence et al. (1967) studied nitrogen fixation ($^{15}N_2$) by Dryas drummondii, an important colonist at Glacier Bay, Alaska, in greenhouse experiments. Stewart and Pearson (1967) examined dinitrogen fixation ($^{15}N_2$) in Hippophae rhamnoides on sand dunes in eastern England. Skeffington and Bradshaw (1980) examined nitrogen fixation rates (C_2H_2 reduction) associated with leguminous

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species (e.g. Lupinus arboreus) and non-leguminous species (e.g. Agrostis tenuis), and nitrogen accumulation during the natural development of ecosystems on china clay waste in England.

At Glacier Bay, Alaska (59 °N, 136.5 °W), Crocker and Major (1955) found that total soil nitrogen increased by a factor of 45 during the first 100 years of glacial retreat, while Sondheim and Standish (1983) reported a 10-fold increase at Robson Glacier, British Columbia (53.1 °N, 119.1 °W) for a comparable length of time. At the Herbert and the Mendenhall glaciers in Alaska (58.5 °N, 134 °W), total soil nitrogen increased 6-fold during the first 120 years after glacial retreat (Crocker and Dickson 1957). During the first 300 years of dune succession along the southern shore of Lake Michigan (41.5 °N, 87.5 °W), total soil nitrogen increased approximately 15-fold (Olson 1958).

Tilman (1982) has proposed a resource ratio hypothesis for primary succession which predicts that succession is directional or predictable only to the extent that the relative supply rates of limiting resources change in a directional or predictable manner. If this hypothesis is correct, then the rates of biological nitrogen production by nitrogen-fixing organisms will strongly influence the rate of plant succession on the Robson moraines.

The objective of this study was to estimate the rate of biological dinitrogen fixation in successional plant communities on the Robson moraine chronosequence.

6.2 Site Description

Mount Robson (3954 m) is the tallest mountain in the Canadian Rockies and supports a major ice and snow field. The Robson Glacier,

the largest on Mount Robson, has deposited a terminal moraine and approximately 10 recessional moraines during the past 200 years (Plate 2-1). The Robson moraines (53.1 °N, 119.1 °W) are situated at an elevation of 1662 ± 14 m. The moraines under study are 1.49, 1.17, and 0.66 km north (315°) from the terminus of the glacier, and are referred to as moraines 1, 5, and 8, respectively. These recessional moraines were formed in approximately 1801, 1912, and 1939 (Heusser 1956).

The vegetation on these moraines is representative of three phases of plant community development found on this chronosequence. The first phase, the "pioneer" successional community, was dominated by Hedysarum boreale var. mackenzii Nutt. (Rich.)*, the low shrubs Salix vestita Pursh and Salix glauca L. (<1 m in height) and the dwarf shrub Dryas drummondii Richards. (<0.1 m in height). The second phase of successional plant community development found on moraines 7 and 5 were dominated by D. drummondii, H. boreale and the low shrub S. glauca. Picea englmannii Parry ex Engelm. was beginning to emerge above the Salix on moraine 5. The third phase, the oldest plant communities on the Robson moraines were found on moraines 3 and 1. They were dominated by P. engelmannii, the dwarf shrub Arctostaphylos rubra (Rehder & Wils.) Fern., H. boreale, the bryophyte Brachythecium sp., and the lichens Cladonia cariosa (Ach.) Spreng and C. pyxidata (L.) Hoffm.

No climatic data are available for the immediate area of Mount Robson. The nearest weather station is at Red Pass Junction, 20.2 km

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* Nomenclature follows Ireland et al. (1980), Moss (1983), and Egan (1987).

to the southeast of the mountain at an elevation of 1059 m. Mean daily temperature and total precipitation at this station are 1.7 °C and 742.6 mm. Approximately 54% of the total precipitation occurs as snowfall (Anonymous 1982a and b). The climate at the study site is undoubtedly colder and wetter than Red Pass Junction due to greater elevation.

Soil development on the Robson moraines was first described by Tisdale et al. (1966) and more recently by Sondheim and Standish (1983). In general, the soils are well drained loams with a 40 to 70% coarse fragment (>2 mm) content. Orthic Regosols occur on the more recently formed moraines while Orthic Eutric Brunisols have developed on the oldest moraine (Sondheim and Standish 1983). All soils are highly calcareous (76-86% $CaCO_3$ equivalent) and slightly alkaline (pH 7.75 to 7.95). On the oldest recessional moraine both soil organic matter and soil nitrogen content are approximately 10 times greater than that on the youngest (Sondheim and Standish 1983). The build-up of total soil nitrogen occurs in three phases. There is a phase of slow nitrogen accumulation during the first 50 years of colonization, followed by a rapid accumulation phase from 50 to 100 years, and finally a plateau phase of slow decline from 100 to 200 years (Figure 6-1).

6.3 Potential Nitrogen-Fixing Organisms

These phases of nitrogen accumulation correlate well with the abundance of the potential nitrogen-fixing plants, Hedysarum boreale and Dryas drummondii, which attain their peak cover during the phase of rapid accumulation.

Worley (1973) has described a black crustal development in the early stages of primary succession at Glacier Bay, Alaska. He applied the term 'black crust' to at least three separate crust types on recently deglaciated surfaces: a) Cyanophyta mats composed principally of either a film of Scytonema and Nostoc overgrowing moss colonies, or of Gloeocapsa and Phormidium on mineral substrate surfaces; b) mats of the leafy liverwort Lophozia badensis (Gott.) Schiffn. which may be filled with blue-green algae (e.g., Nostoc sp.); and c) lichen mats.

Nostoc sp. (e.g., N. commune Vauche), a potential nitrogen-fixing organism, appears to be most commonly associated with mosses on the early recessional moraines, which suggests that mosses may be sites of nitrogen fixation. Mosses attain their peak cover 80 to 100 years after colonization (Chapter 2). Gloeocapsa sp. is found growing as a 'black crust' on the mineral substrate surface of the youngest moraine.

Fourteen species of lichens are known to colonize the Robson moraines and form an important component of the understory vegetation on the older moraines (Chapter 2). Some of these lichens (e.g., Peltigera aphthosa (L.) Willd., P. rufescens (Weis) Humb., Panneria pezizoides (Weber) Trevisan, Solarina saccata (L.) Arch, and Stereocaulon sp.) are known to fix nitrogen (Millbank 1976). The most abundant lichens on the older recessional moraines are Cladonia cariosa and C. pyxidata but have not been reported to fix nitrogen. The lichen Rinodina turfacea (Wahlenb.) Korber forms a 'black crust' on the older moraines.

Barbilophozia lycopodioides (Wallr.) Loesk., and Lophozia sp. also colonize the older moraines. Examination of these hepatics with a

hand lens revealed the presence of colonies of Nostoc sp. among the thalli, indicating that hepatics may be sites of nitrogen fixation. However, these leafy hepatics do not form a 'black crust' on the Robson moraines as they do at Glacier Bay, Alaska (Worley 1972).

The shrub Shepherdia canadensis (L.) Nutt. bears nitrogen-fixing nodules (McNabb and Geist 1979) and the dwarf shrub Dryas octopetala L. is known to be nodulated (Lawrence et al. 1967) but has not been reported to fix nitrogen (Waughman et al. 1981). Both are late colonizers on the Robson moraines. Dryas integrifolia M. Vahl also colonizes the moraines and has recently been reported to fix nitrogen (Henry and Svoboda 1986). Arctostaphylos uva-ursi, an early colonizer on the Robson moraines, was thought to have nitrogen-fixing root nodules (Allen et al. 1964; Bond 1974) but was later reported to be mycorrhizal (Becking 1974) or have vegetative buds (see Bond and Wheeler 1980).

6.4 Methods

Recessional moraines 8, 5, and 1, representing three phases of plant community development, were sampled for their nitrogen-fixing potential using the acetylene reduction technique (Stewart et al. 1967). Samples of potential nitrogen-fixing organisms (Hedysarum boreale var. mackenzii; Dryas drummondii; D. octopetala; Shepherdia canadensis; Nostoc commune; the mosses, Tortella inclinata (Hedw.) Limpr., Bryum sp., and Ditrichum flexicaule (Schwaegr.) Hampe. in association with N. commune; the lichens, Peltigera aphthosa, P. rufescens, Cladonia pyxidata, C. cariosa and Rinodina turfacea; and free-living soil micro-organisms (e.g., Gloeocapsa sp.) were placed in

either 435, 465, 980, or 1700 ml glass canning jars and sealed with lids fitted with butyl rubber stoppers. Within approximately 15 minutes of collecting the sample, air was removed by syringe from the jar and purified acetylene was introduced to give a 9:1 v/v air acetylene mixture. After 1 hour, a 10 ml gas sample was removed and injected into a 100x16 mm Vacutainer tube (Becton/Dickenson) which had previously been opened, aired and re-evacuated to remove contaminating gases (Marowitch et al. 1987). The selection of a short incubation period was based on recommendations by Hardy and Holsten (1977), Sloger (1980), Knowles (1980), and Silvester(1983). After 1 to 3 weeks, samples of 1 ml were removed from the tubes and analyzed for acetylene and ethylene with a Hewlett-Packard 5880 gas chromatograph, fitted with a Poropak Q column (3.05 m) and a flame ionization detector.

Total ethylene (µmol) was estimated by the method of Turner and Gibson (1980). An ethylene standard (µmol/unit area under peak in calibration curve) was determined for each assay vessel from the average of 19 to 20 injections of a known volume of pure ethylene.

Samples were collected four times during the 1986 field season, July 3-7, July 17-23, July 31-August 9, and August 14-22 on moraine 8 and the last three times on moraines 5 and 1. Barbilophozia lycopodioides was sampled between August 14 and 22. Shepherdia canadensis was sampled between August 14 and 22, 1986, and between July 2 and 6, 1987, on moraine 1. Dryas drummondii and D. octopetala were sampled between July 3 and 7, 1986, on 7. A minimum of six samples of each organism were collected during each sample period. Five samples were incubated with acetylene and one was used as an

uninnoculated control to determine natural ethylene production. Ethylene was not detected in any of the controls, and thus ethylene production was a product of acetylene reduction.

Whole plants of H. boreale, S. canadensis, D. drummondii, and D. octopetala were excavated and incubated in buried jars to approximate true soil temperatures. Care was taken to remove soil adhering to the roots and to ensure that nodules remained attached to the roots. Excision of roots from shoots of crop legumes is believed to significantly depress ethylene production (Smith and Hume 1987). However, Grove and Malajczuk (1987) found that excision had no significant effect on rates of ethylene production in forest legumes.

Each moraine was divided into 3 sections (lower, mid, and upper slope), and within each section, samples were taken at regularly spaced intervals to ensure that a range of sites were sampled. Due to the difficulty of excavating S. canadensis with intact root nodules, samples were removed where they could be found.

Soil cores (5.5 cm x 5 cm deep) from vegetated and unvegetated sufaces were incubated in buried jars to simulate soil temperatures. Moss and lichen cores were incubated in jars left 5 cm above ground level to allow sunlight to enter for photosynthesis. The lichen samples were moistened with a few drops of water. Thalli of Nostoc commune, sufficient to cover the bottom of the incubation vessel, were collected from the bottom mud of several temporary ponds. The incubation jars were placed in a pool of water to allow light penetration and temperature equilibration.

The abundance of organisms which were examined for nitrogen fixation was determined for each moraine as part of a vegetation study

(see Chapter 2). Eight 25 m^2 quadrats, each containing 5 contiguous 1 m^2 quadrats, were preferentially located on moraine 8 and 10 were located on moraines 5 and 1. The density of S. canadensis was determined on moraine 1 from 14 randomly placed 25 m^2 quadrats. No attempt was made to determine the abundance of Nostoc commune and Gloeocapsa sp.

The number of nodules per plant on each moraine was determined for Hedysarum boreale by excavating 20 randomly selected plants, and for Shepherdia canadensis by excavating 17 randomly selected plants. For Dryas drummondii and D. octopetala, 30 plants were excavated.

Surface and soil temperatures (5, 10, 15 and 25 cm depth) on moraine 8 were monitored hourly throughout the field season using thermistors and an automated data logging system (Campbell Scientific CR5). Temperatures of the buried incubation jars and adjacent soil were also measured periodically. Differences between the jars and adjacent soil ranged from -1 to +5 °C.

Air temperature was recorded by Belfort hygrothermograph and precipitation by Taylor rain guage on moraine 1 during July and August 1985 and 1986. The hygrothermograph was housed in a Stevenson Screen (base height 115 cm). The rain gauge rim height was 41 cm.

Mean rates of ethylene production ($\mu mol\ m^{-2}\ h^{-1}$) for each organism on each moraine were calculated for the entire field season. Mean rates of ethylene production were adjusted for cover (%) to determine total rates of ethylene production for each organism by moraine. For conversion of acetylene production to dinitrogen fixation, the theoretical ratio (3:1) was used (Minchin et al. 1983). Estimates of annual nitrogen input from each moraine were based on a daily 8 hour

nitrogen-fixing period (mean hourly air temperature >10 °C) and an estimated 90-day growing season.

6.5 Results

Temperature and Precipitation Data

The 1985 mean daily air temperature and precipitation for July and August were 11.1 °C and 16.3 mm and 7.5 °C and 86.1 mm, respectively. The 1986 mean daily temperature and precipitation for July was 7.4 °C and 75.5 mm and for August 1-23 was 9.3 °C and 10.5 mm.

The mean and range of surface and soil temperatures for the July and August 1986 incubation period are shown in Table 6-1.

Acetylene Reduction Activity

A summary of the mean seasonal acetylene reduction activity for each moraine by all potential nitrogen-fixing organisms is given in Table 6-2.

On recessional moraine 8 the highest activity rates were found for colonies of the blue-green alga Nostoc commune (109.04 ± 23.13 μmol m^{-2} h^{-1}) in ponds, which was almost twice that of the legume Hedysarum boreale (57.47 ± 11.47 μmol m^{-2} h^{-1}). Nostoc in association with mosses, and soil cores in vegetated areas showed comparable acetylene reduction activities (23.52 ± 4.32 and 26.05 ± 8.69 μmol m^{-2} h^{-1}, respectively) followed by soil cores in unvegetated areas (19.80 ± 10.15 μmol m^{-2} h^{-1}). Blue-green algae colonies were noted in three of the soil cores, suggesting that N. commune may also be an important nitrogen-fixing organism in soils on the younger moraines.

On the intermediate moraine 5, H. boreale showed the highest acetylene reduction activites (45.66 ± 5.71 μmol m^{-2} h^{-1}) followed by

soil cores in vegetated areas (17.74 ± 3.41 μmol m^{-2} h^{-1}). Nostoc associated with mosses, and soil cores in unvegetated areas, showed comparable acetylene reduction activities (3.35 ± Ø.74 and 2.95 ± Ø.7Ø μmol m^{-2} h^{-1}, respectively) (Table 6-2).

No nodules were found on the roots of Dryas drummondii or D. octopetala. As a consequence, the acetylene reduction activity of D. drummondii (1.97 ± 1.22 μmol m^{-2} h^{-1}) and D. octopetala (1.14 ± Ø.76 μmol m^{-2} h^{-1}) were very low. Tisdale et al. (1966) reported finding nodules on the roots of Dryas at the site, as well as on Hedysarum boreale. They found that nodules on Dryas were about one quarter of the abundance of nodules found on Hedysarum. During this study, nodules were sometimes found among the roots of D. drummondii, but were never found attached to the main root stock. Based on a Dryas to Hedysarum nodule ratio of 1:4 (Tisdale et al. 1966), and estimates from this study of 4Ø, 8, and 3 nodules per plant for Hedysarum on moraines 8, 3, and 1, one would expect to find a small number of nodules on Dryas roots (Ø.79 nodules per plant on moraine 1, 1.6 nodules per plant on moraine 5 and 1Ø nodules per plant on moraine 8). It is conceivable that nodules on the roots of Dryas could go undetected on moraines 1 and 5 due to their diffuse pattern of nodulation (Lawrence et al. 1967) and the degree of difficulty of excavating intact root systems. However, the latter was much less of a problem on the younger moraine 8 and still no nodules were found. Therefore, from the findings from this study and Tisdale et al. (1966) it appears that D. drummondii and D. octopetala are not nodulated on the younger moraines and only to a small extent on the older moraines.

On the oldest recessional moraine, highest mean rates of acetylene reduction were found for the lichens Peltigera aphthosa and P. rufescens (24.84 ± 13.60 and 6.96 ± 3.36 μmol m^{-2} h^{-1}). Much lower levels of acetylene reduction were found for the remaining organisms on moraine 1 (Table 6-2). Shepherdia canadensis had the lowest mean rates of acetylene reduction on the moraines (Table 6-2). This may be a result of several factors. Only saplings of S. canadensis (shoots 12-40 cm in height, roots 10-27 cm in length) could be incubated due to the volume restriction of the incubation vessels. Some of the nodules of S. canadensis appeared to be old and in poor condition (26% of the nodule meristems were darkened in colour). This is in marked contrast to the fleshy creamy-yellow nodule clusters found on Hedysarum boreale roots. Also, the low levels of ethylene production may be due to a lag phase in acetylene reduction. Gas samples removed from the same incubation vessel after a 1/2 hour, 1 hour and 2 hour periods showed a 24% (n=3) increase in ethylene. This is in contrast to the vigorous ethylene production and increases of 100% for soil cores (n=2) and H. boreale (n=6) after a 1/2 hour and 1 hour period.

The estimated mean cover (%) of unvegetated and vegetated soil, ponds, mosses and potential nitrogen-fixing organisms on the Robson moraines is summarized in Table 6-3. The highest total rate of ethylene production on all the moraines was on the youngest recessional moraine (8). Hedysarum boreale made the greatest contribution (57.47 ± 11.77 μmol m^{-2} h^{-1}) to the total ethylene production on moraine 8 followed by unvegetated soil (15.73 ± 8.06 μmol m^{-2} h^{-1}) (Table 6-4). Nostoc, free living in ponds and in association with mosses on land, made only small contributions to the

total ethylene production (Ø.981 ± Ø.208 and Ø.53 ± Ø.10 µmol m^{-2} h^{-1}, respectively) because of their low cover on the moraine (Table 6-3). On moraine 5, H. boreale made the greatest contribution to the total ethylene production (45.66 ± 5.71 µmol m^{-2} h^{-1}) followed by vegetated and unvegetated soil (1Ø.22 ± 1.96 and 1.21 ± Ø.29 µmol m^{-2} h^{-1}, respectively). The lowest total rate of ethylene production was found on moraine 1. Hedysarum boreale made the greatest contribution to the total ethylene production (8.91 ± 1.73 µmol m^{-2} h^{-1}) followed by vegetated soil (Ø.77 ± Ø.37 µmol m^{-2} h^{-1}), and Nostoc associated with mosses (Ø.232 ± Ø.Ø78 µmol m^{-2} h^{-1}). Peltigera aphthosa and P. rufescens only made small contributions to the total rate of ethylene production (Ø.Ø12 ± Ø.ØØ7 and Ø.Ø31 ± Ø.Ø15 µmol m^{-2} h^{-1}, respectively) because of their low cover (Table 6-3). Cladonia spp. made a small but higher contribution than Peltigera to total ethylene production (Ø.1ØØ ± Ø.Ø57 µmol m^{-2} h^{-1}) because of its higher cover (Table 6-3). The remaining organisms contributed little (Table 6-4) due to their low mean ethylene production (Table 6-2) and cover (Table 6-3).

The estimated annual N input from nitrogen fixation on the Robson moraines is shown in Table 6-5. The highest values were on the youngest moraine (534 mg N m^{-2} yr^{-1}) and decreased to a low of 68 mg N m^{-2} yr^{-1} on the oldest moraine. Hedysarum boreale contributed the majority of nitrogen on all three moraines 8, 5, and 1 (72, 79, and 87%, respectively) followed by soil micro-organisms (26, 20, and 8%, respectively). All the other organisms made a minor contribution to the estimated annual N input (Table 6-5).

6.6 Discussion

There are few studies that have examined biological nitrogen fixation in relation to primary succession (see Waughman et al. 1981). In addition, a variety of techniques have been used to assess nitrogen fixation (i.e., acetylene reduction, isotopic studies, N balance and biomass accretion) making direct comparison of results difficult. However, when total soil nitrogen is low (<0.1%), the majority of nitrogen in diazotrophs is generally due to fixation, and estimates of accretion and nitrogen-fixation are comparable (Silvester 1983).

At Glacier Bay, Alaska, the early colonizer Dryas drummondii accumulated 762 mg $N\ m^{-2}\ yr^{-1}$ over a 40 year period (Lawrence et al. 1967) and up to 1236 mg $N\ m^{-2}\ yr^{-1}$ over 25 years, while the secondary colonizer Alnus crispa accummulated 6800 mg $N\ m^{-2}\ yr^{-1}$ over a 40 year period (Crocker and Major 1955). At Glacier Bay, Dryas is less effective than A. crispa in building up soil nitrogen, but is important in places where Alnus is absent (Lawrence et al. 1967). On recessional moraines of the Athabasca Glacier, Alberta (52.2 °N, 117.2 °W), Fitter and Parsons (1987) found that D. drummondii was not nodulated and speculated that the slow accumulation of soil nitrogen was due to a lack of symbiotic fixation. Dryas drummondii does not appear to be nodulated on the Robson moraines and is a dominant early colonizer on the moraines. To compare properly the N input of D. drummondii on the Robson moraines with that at Glacier Bay and on the Athabasca moraines, the net amount of biological nitrogen contributed would have to be based on estimates of biomass accretion. It is hypothesized that Hedysarum boreale var. mackenzii has a primary role similar to A. crispa at Glacier Bay, whereas soil micro-organisms

(e.g., Gloeocapsa sp.) and blue-green algae (e.g., Nostoc commune) appear to play a secondary role similar to that of D. drummundii at Glacier Bay.

Nitrogen fixation by herbaceous legumes during primary succession on abandoned mine spoils has been investigated (Skeffington and Bradshaw 1980) but to the best of my knowledge, has not been previously examined in natural primary succession. Skeffington and Bradshaw (1980) found that nitrogen fixation rates associated with leguminous species were ten times greater than that of non-leguminous species and were the most effective of all the species in the promotion of nitrogen accumulation in the reclamation of china clay waste in England. Intensive studies of the nutritional role of the tree lupin Lupinus arboreus in coastal sand dune forestry in New Zealand showed that the lupin contributed approximately one-quarter of the nitrogen required for Pinus radiata growth (Sprent and Silvester 1973; Sprent 1973). Jefferies et al. (1981) found that nitrogen accumulated by Trifolium repens may become available to associated species on nutrient deficient mine spoils. They found that the biomass of the companion grass Agrostis castellana sown with the legume was 4.75 times that of the grass grown in monoculture. Hedysarum boreale may play a similar role on the Robson moraines. Salix glauca, Salix seedlings, and Picea engelmannii were found more often within clumps of H. boreale than not, suggesting that H. boreale may provide "safe sites" and facilitate establishment and growth (see Chapter 4).

Skujins et al. (1987) examined dinitrogen fixation in a Picea engelmannii secondary succession. They found that Lupinus argenteus

made a marked contribution (55%) to the nitrogen input in the intermediate Populus tremuloides stage, which was lower than the nitrogen contribution made by H. boreale (79%) on intermediate recessional moraine 5. However, the mean nitrogen-fixation rate by H. boreale of 3.22 ± 0.40 µmol C_2H_4 h^{-1} per plant was very similar to that of L. argenteus (3.12 ± 1.64 µmol C_2H_4 h^{-1} per plant).

The annual input (68 mg N m^{-2} yr^{-1}) on the 185 year old recessional moraine 1, which was dominated by Picea engelmannii, was very similar to that found in an Australian Pinus radiata forest where litter and soil micro-organisms fixed 64 mg N m^{-2} yr^{-1} (Baker and Attiwell 1984). This value was higher than that found in a 120 year old Swedish Pinus silvestris forest where free-living nitrogen-fixing micro-organisms added 35 mg N m^{-2} yr^{-1} (Granhall and Lindberg 1978), and was also greater than that found in a subalpine P. engelmannii forest in Utah where symbiotic and non-symbiotic nitrogen-fixing micro-organisms added 32 mg N m^{-2} yr^{-1} (Skujins et al. 1987). However, N-input on this oldest moraine was much lower than that found in a mixed Picea abies and Pinus silvestris stand in Sweden where free-living micro-organisms, principally blue-green algae in association with Sphagnum mosses, fixed 320 mg N m^{-2} yr^{-1} (Granhall and Lindberg 1978).

Stewart and Pearson (1967) examined nitrogen fixation ($^{15}N_2$) by Hippophae rhamnoides (Elaeagnaceae) a dominant colonizer on sand dunes in eastern England. They found nitrogen fixation increased from 440 mg N m^{-2} yr^{-1} on embryo dunes to 5780 mg N m^{-2} yr^{-1} on intermediate successional dunes and declined considerably on the mature dunes to 150 mg N m^{-2} yr^{-1}. A similar trend has been reported by Skujins et

al. (1987) for a subalpine secondary succession. They found that dinitrogen-fixation (C_2H_2) increased from 33 mg N m^{-2} yr^{-1} in the early subalpine meadow stage to 115 mg N m^{-2} yr^{-1} in the intermediate aspen stage and fell to 32 mg N m^{-2} yr^{-1} in the late successional Picea engelmannii stage. They concluded that the decrease of nitrogen fixation could be another mechanism "tightening" the nitrogen cycle in late successional communities. On the Robson moraines examined, peak nitrogen fixation occurred on recessional moraine 8 (51 years old) and declined to a low on the late recessional moraine 1. Thus the overall trend appears to be a marked drop in nitrogen fixation in the mature communities. These results are consistent with the trends to be expected in ecological succession by Odum (1969), Vitousek and Reiners (1975), and Gorham et al. (1979). In less than 200 years, total soil nitrogen on the Robson moraines appears to have reached a temporary steady state, where rates of change are relatively low (Sondheim and Standish 1983). Decreased nitrogen fixation could be one mechanism which helps to maintain this steady state.

Figure 6-1. Percent total nitrogen of soils (0-15 cm depth) on the Robson moraines (from Sondheim and Standish 1983). The position of the recessional moraines (RM) sampled and the major phases of vegetation development are shown. The phases of vegetation development are labeled as:

I. Pioneer *Hedysarum*

II. *Dryas* transition

III. *Picea*

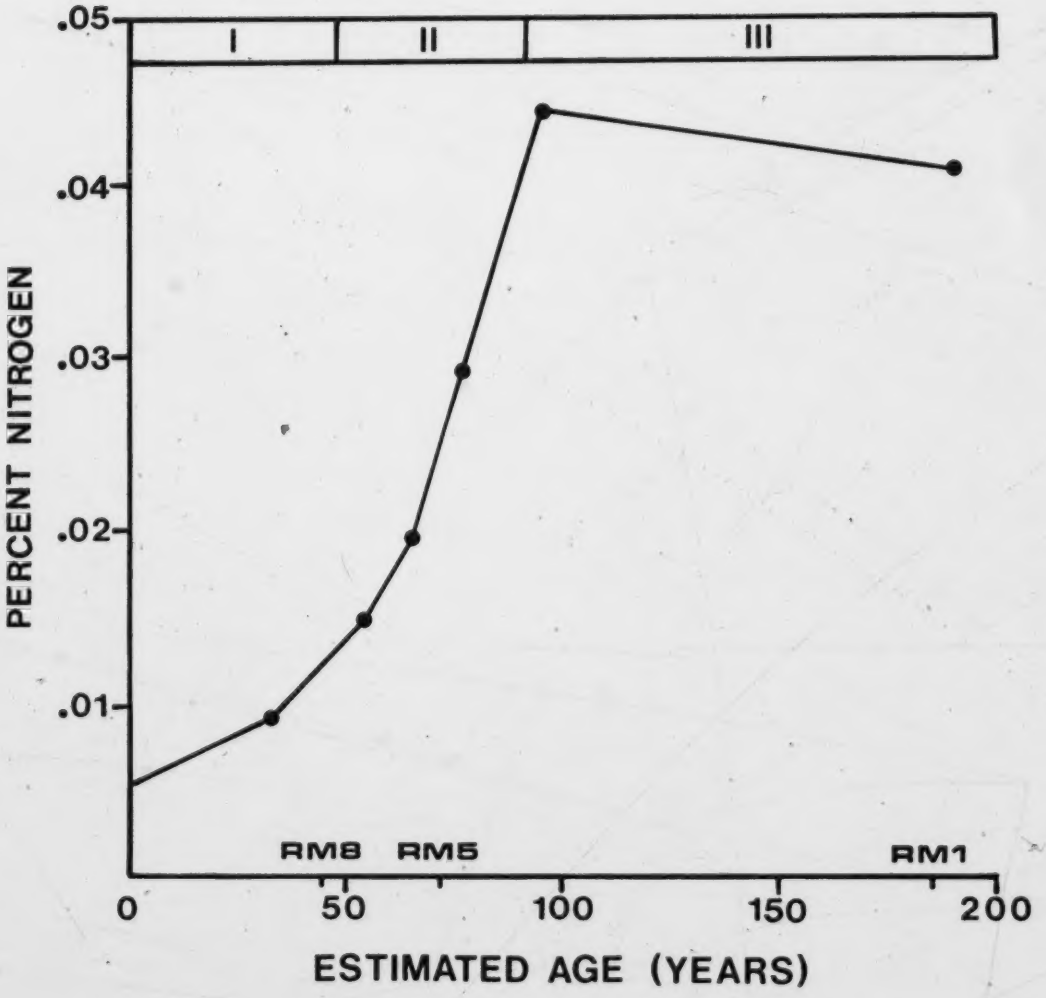

.05
.04
.03
.02
.01
I
II
III
PERCENT NITROGEN
RM8
RM5
RM1
0
50
100
150
200
ESTIMATED AGE (YEARS)

Table 6.1. Mean and range of surface and soil temperatures (^{o}C) for the July and August 1986 incubation period on recessional moraine 8.

	SOIL DEPTH (cm)				
MONTH	0	5	10	15	25
JULY 3-7	9.6 (6.6-12.8)	9.7 (7.0-12.4)	9.3 (7.2-11.6)	9.2 (7.2-11.4	8.9 (8.0-10.2)
JULY 18-23	12.6 (10.9-14.0)	12.7 (11.6-14.0)	12.4 (11.0-13.7)	12.0 (10.6-13.5)	11.6 (9.4-12.7)
JULY 31-AUG.9	12.9 (11.8-14.8)	12.9 (11.5-14.8)	12.9 (12.1-14.4)	12.8 (12.0-14.3)	12.4 (11.5-13.3)
AUGUST 13-21	12.5 (10.8-14.0)	12.1 (10.4-13.3)	12.2 (10.7-13.2)	11.9 (10.8-13.2)	12.1 (11.5-12.9)

Table 6-2. Mean rate of ethylene production (± S.E.) and number of samples on the Robson moraines.

	RECESSIONAL MORAINE		
	Young	Intermediate	Old
	8	5	1
ORGANISM	µMol C_2H_4 m^{-2} h^{-1}		
Soil:			
unvegetated	19.80 (10.15) n=25	2.95 (0.70) n=15	—
vegetated	26.05 (8.69) n=20	17.74 (3.41) n=14	0.79 (0.38) n=15
Nostoc commune:			
free living in ponds	109.04 (23.13) n=27	—	—
associated with mosses	23.52 (4.32) n=83	3.35 (0.74) n=55	1.45 (0.49) n=36
Lichens:			
Peltigera aphthosa	—	—	24.84 (13.60) n=16
P. rufescens	—	—	6.96 (3.36) n=15
Cladonia sp.	—	—	1.59 (0.90) n=15
Rinodina turfacea	—	—	1.51 (0.96) n=15
Liverwort:			
Barbilophozia lycopodioides	—	—	0.532 (0.403) n=5
Vascular plants:			
Dryas drummondii	—	1.97 (1.22) n=15	—
D. octopetala	—	1.14 (0.76) n=9	—
Shepherdia canadensis	—	—	0.015 (0.003) n=50
Hedysarum boreale var. *mackenzii*	57.47 (11.77) n=51	45.66 (5.71) n=29	8.91 (1.73) n=23

Table 6-3. Estimated mean cover (%) of unvegetated and vegetated soil, ponds, mosses and liverworts, lichens and Dryas. Estimated density (plants m^{-2}) and number of nodule meristems per plant are shown for Shepherdia canadensis and Hedysarum boreale.

	RECESSIONAL MORAINE		
ORGANISM	8	5	1
Soil:			
unvegetated	79.45 (5.06)	41.20 (3.92)	0.05 (0.05)
vegetated	18.00 (4.76)	47.60 (3.90)	98.00 (0.94)
Ponds	0.90	—	—
Mosses	2.26 (1.13)	12.02 (3.55)	15.97 (3.06)
Lichens:			
Peltigera aphthosa	—	—	0.05 (0.05)
P. rufescens	0.05 (0.03)	—	0.45 (0.25)
Cladonia sp.	—	—	6.32 (1.97)
Rinodina turfacea	—	0.09 (0.05)	0.96 (0.61)
Liverwort:			
Barbilophozia lycopodioides	—	—	0.52 (0.28)
Vascular plants:			
Dryas drummondii	4.37 (2.29)	13.13 (3.76)	0.01 (0.01)
D. octopetala	1.08 (0.69)	1.42 (0.70)	3.77 (1.17)
Shepherdia canadensis (plants m^{-2})*	—	—	0.39 (0.06)
Hedysarum boreale var. mackenzii (plants m^{-2})+	5.58 (0.80)	14.18 (1.58)	7.80 (1.21)
*nodule meristems per plant	—	—	11.12 (6.28)
+nodule meristems per plant	80.30 (27.65)	16.10 (3.48)	6.30 (2.03)

Table 6-4. Total rate of ethylene production (± S.E.) on the Robson moraines.

ORGANISM	RECESSIONAL MORAINE 8	5	1
	μMol C_2H_4 $m^{-2} h^{-1}$		
Soil:			
unvegetated	15.73 (8.06)	1.21 (0.29)	—
vegetated	4.69 (1.56)	10.22 (1.96)	0.77 (0.37)
Nostoc commune:			
free living in ponds	0.981 (0.208)	—	—
associated with mosses	0.530 (0.100)	0.403 (0.089)	0.232 (0.078)
Lichens:			
Peltigera aphthosa	—	—	0.012 (0.007)
P. rufescens	0.003 (0.002)	—	0.031 (0.015)
Cladonia sp.	—	—	0.100 (0.057)
Rinodina turfacea	—	0.001 (0.001)	0.014 (0.009)
Liverwort:			
Barbilophozia lycopodioides	—	—	0.012 (0.007)
Vascular plants:			
Dryas drummondii	0.086 (0.053)	0.259 (0.160)	—
D. octopetala	0.012 (0.008)	0.016 (0.011)	0.043 (0.029)
Shepherdia canadensis	—	—	0.065 (0.013)
Hedysarum boreale var. *mackenzii*	57.47 (11.77)	45.66 (5.71)	8.91 (1.73)
TOTAL	79.502	57.769	10.189

Table 6-5. Estimated N input from dinitrogen fixation on the Robson moraines

	Dinitrogen Fixation (mg N m^{-2} yr^{-1})		
	RECESSIONAL MORAINE		
ORGANISM	8	5	1
Soil microorganisms	137.2	76.8	5.2
Algae	10.1	2.7	1.6
Liverwort	—	—	0.1
Lichens	—	—	1.0
Shepherdia canadensis	—	—	0.4
Dryas sp.	0.6	1.8	0.3
Hedysarum boreale var. *mackenzii*	386.2	306.8	59.9
TOTAL	534.1	388.1	68.5

6.7 References

Allan, E.K., O.N. Allen and L.J. Klebesadel. 1964. An insight into symbiotic nitrogen-fixing plant associations in Alaska. Science in Alaska. In: Proc. 14th Alaskan Sci. Conf., Anchorage, Alaska. pp 54-63.

Anonymous. 1982a. Canadian Climate Normals 1951-1980. Temperature. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 306 pp.

Anonymous. 1982b. Canadian Climate Normals 1951-1980. Precipitation. Canadian Climate Program, Environment Canada, Atmospheric Environment Service, Downsview, Ont. 602 pp.

Baker, T.G. and P.M. Attiwill. 1984. Acetylene reduction in soil and litter from pine and eucalyptus forests in south-eastern Australia. Soil Bio. Biochem. 16: 241-245.

Becking, J.H. 1977. Dinitrogen-fixing associations in higher plants other than legumes. In: A Treatise on Dinitrogen Fixation. Section III: Biology. Edited by R.W.F. Hardy and W.S. Silver. John Wiley and Sons, Toronto, Ont. pp 185-275.

Black, C.A. 1968. Soil-Plant Relationships. Second Edition. John Wiley and Sons, Toronto, Ont. 792 pp.

Bond, G. 1974. Root-nodule symbioses with actinomycete-like organisms. In: The Biology of Nitrogen Fixation. Edited by A. Quispel. American Elsevier Publ. Co., Inc., New York, NY. pp

342-378.

Bond, G. and C.T. Wheeler 1980. Non-legume nodule systems. In: Methods for Evaluating Biological Nitrogen Fixation. Edited by F.J. Bergersen. John Wiley and Sons, Toronto, Ont. pp 185-211.

Cooper, W.S. 1916. Plant succession in the Mount Robson region, British Columbia. Plant World 19: 211-238.

Crocker, R.L. and B.A. Dickson. 1957. Soil development on the recessional moraines of the Herbert and Mendenhall glaciers, southeastern Alaska. J. Ecol. 45: 169-185.

Crocker, R.L. and J. Major. 1955. Soil development in relation to vegetation and surface age at Glacier Bay, Alaska. J. Ecol. 43: 427-448.

Dickson, B.A. and R.L. Crocker. 1953. A chronosequence of soils and vegetation near Mount Shasta, California. II. The development of the forest floors and the carbon and nitrogen profiles of the soils. J. Soil Sci. 4: 142-154.

Egan, R.S. 1987. A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. The Bryologist 90: 77-173.

Fitter, A.H. and W.F.J. Parsons. 1987. Changes in phosphoros and nitrogen availability on recessional moraines of the Athabasca Glacier, Alberta. Can. J. Bot. 65: 210-213.

Gorham, E., P.M. Vitousek and W.A. Reiners. 1979. The regulation of

chemical budgets over the course of terrestrial ecosystem succession. Ann. Rev. Ecol. Syst. 10: 53-84.

Granhall, U. and T. Lindberg. 1978. Nitrogen fixation in some coniferous forest ecosystems. In: Environmental Role of Nitrogen-fixing Blue-green Algae and Asymbiotic Bacteria. Edited by U. Grandhall. Ecol. Bull. (Stockholm) 26: 178-192.

Grove, T.S. and N. Malajczuk. 1987. Nitrogen fixation (acetylene reduction) by forest legumes: Sensitivity to pre-harvest and assay conditions. New Phytol. 106: 115-127.

Hardy, R.W.F. and R.D. Holsten. 1977. Methods for measurement of dinitrogen fixation. In: A Treatise on Dinitrogen Fixation. Section IV: Agronomy and Ecology. Edited by R.W.F. Hardy and A.H. Gibson. John Wiley and Sons, Toronto, Ont. pp 451-486.

Henry, G.H.R. and J. Svoboda. 1986. Dinitrogen fixation (acetylene reduction) in high arctic sedge meadow communities. Arctic and Alpine Res. 18: 181-187.

Heusser, C.J. 1956. Post glacial environments in the Canadian Rocky Mountains. Ecol. Monogr. 26: 263-302.

Ireland, R.R., C.D. Bird, G.R. Brassard, W.B. Schofield and D.H. Vitt. 1980. Checklist of the mosses of Canada. Publications in Botany, No. 8. Ottawa, Ont. 75 pp.

Jacobson, G.L. and H. J. B. Birks. 1980. Soil development on recent end moraines of the Klutlan Glacier, Yukon Territory, Canada.

Quaternary Res. 14: 87-100.

Jefferies, R.A., A.D. Bradshaw and P.D. Putwain. 1981. Growth, nitrogen accumulation and nitrogen transfer by legume species established on mine spoils. J. Appl. Ecol. 18: 945-956.

Jenny, H. 1980. Soil Genesis with Ecological Perspectives. Ecological Studies No. 37. Springer-Verlag, New York, NY.

Knowles, R. 1980. The measurement of nitrogen fixation. In: Current Perspectives in Nitrogen Fixation. Proc. 4th Inter. Symp. on Nitrogen Fixation, Canberra, Australia, 1980. Edited by A.H. Gibson and W.E. Newton. Australian Academy of Science, Camberra. pp 327-333.

Lawrence, D.B., R.E. Schoenike, A. Quispel and G. Bond. 1967. The role of Dryas drummondii in vegetation development following ice recession at Glacier Bay, Alaska, with special reference to its nitrogen fixation by root nodules. J. Ecol. 55: 793-813.

Leisman, G.A. 1957. A vegetation and soil chronosequence on the Mesabi iron range spoil banks, Minnesota. Ecol. Monogr. 27: 221-245.

Marowitch, J., M.R.T. Dale and J. Hoddinott. 1988. The effects of crude oil and oil spill chemicals on nitrogen fixation in the Cyanobacteria Nostoc sp. Environ. Pollut. 51: 75-83.

Marrs, R.H., R.D. Roberts, R.A. Skeffington and A.D. Bradshaw. 1981. Nitrogen and the development of ecosystems. In: Nitrogen as an

Ecological Factor. Edited by J.A. Lee, S. McNeill and I.A. Rorison. Blackwell Scientific Publ., Boston, Mass. pp 113-136.

McNabb, D.H. and J.M. Geist. 1979. Acetylene reduction assay of symbiotic N fixation under field conditions. Ecology 60: 1070-1072.

Millbank, J.W. 1976. Aspects of nitrogen metabolism in lichens. In: Lichenology: Progress and Problems. Edited by D.H. Brown, D.L. Hawksworth and R.H. Bailey. Systematic Association, Special Vol. No. 8, Academic Press, New York, NY. pp 441-455.

Minchin, F.R., J.F. Witty, J.E. Sheehy and M. Muller. 1983. A major error in the acetylene reduction assay: decreases in nodular nitrogenase activity under assay conditions. J. Expt. Bot. 34: 641-649.

Moss, E.H. 1983. Flora of Alberta. 2nd ed. (revised by J.G. Packer). University of Toronto Press, Toronto, Ont. 687 pp.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Olson, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Bot. Gaz. 119: 125-169.

Silvester, W.B. 1983. Analysis of nitrogen fixation. In: Biological Nitrogen Fixation in Forest Ecosystems: Foundations and Applications. Edited by J.C. Gordon and C.T. Wheeler. Martinus Nijhoff / Dr W. Junk Pub., Boston, Mass. pp 173-212.

Skeffington, R.A. and A.D. Bradshaw. 1980. Nitrogen fixation by plants grown on reclaimed china waste. J. of Applied Ecology 17: 469-477.

Skujins, J., C.C. Tann and I. Borjesson. 1987. Dinitrogen fixation in a montane forest sere determined by N assimilation and in situ acetylene-reduction methods. Soil Biol. Biochem. 19: 465-471.

Sloger, C. 1981. Associative nitrogen fixation involving cereals and grasses. In: Current Perspectives in Nitrogen Fixation. Proc. 4th Inter. Symp. on Nitrogen Fixation, Canberra, Australia, 1980. Edited by A.H. Gibson and W.E. Newton. Australian Academy of Science, Canberra. pp 321.

Smith, D.L. and D.J. Hume. 1987. Comparison of assay methods for N fixation utilizing white bean and soybean. Can. J. Plant Sci. 67: 11-19.

Sondheim, M.W. and J.T. Standish. 1983. Numerical analysis of a chronosequence including an assessment of variability. Can. J. Soil Sci. 63: 501-517.

Sprent, J.I. and W.B. Silvester. 1973. Nitrogen fixation by Lupinus arboreus in the open and under different aged stands of Pinus radiata. New Phytol. 72: 991-1003.

Sprent, J.I. 1973. Growth and nitrogen fixation in Lupinus arboreus as affected by shading and water supply. New Phytol. 72: 1005-1022.

Stewart, W.D.P., G.P. Fitzgerald and R.H. Burris. 1967. In situ

studies on N_2 fixation using the acetylene reduction technique. Proc. Natl. Acad. Sci. U.S.A. 58: 2071-2078.

Stewart, W.D.P. and M.C. Pearson. 1967. Nodulation and nitrogen-fixation by Hippophae rhamnoides L. in the field. Plant Soil 26: 348-360.

Syers, J.K., J.A. Adams and T.W. Walker. 1970. Accumulation of organic matter in a chronosequence of soils developed on wind-blown sand in New Zealand. J. Soil Sci. 21: 146-153.

Tamm, C.O. 1975. Plant nutrients as limiting factors in ecosystem dynamics. In: Productivity of World Ecosystems. Washington US Nat. Acad. Sci. pp 129-132.

Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press, Princeton, N.J. pp 228-234.

Tisdale, E.W., M.A. Fosberg and C.E. Poulton. 1966. Vegetation and soil development on a recently glaciated area near Mount Robson, British Columbia. Ecology 47: 517-523.

Turner, G.L. and A.H. Gibson. 1980. Measurements of nitrogen fixation by indirect means. In: Methods for Evaluating Biological Nitrogen Fixation. Edited by F.J. Bergersen. John Wiley and Sons, Toronto, Ont. pp 111-138.

Viereck, L.A. 1966. Plant succession and soil development on gravel outwash of the Muldrow Glacier, Alaska. Ecol. Monographs 36: 181-200.

Vitousek, P.M. and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience 25: 376-381.

Vitousek, P.M. and L.R. Walker. 1987. Colonization, succession and resourse availability: ecosystem-level interactions. In. Colonization, Succession and Stability. 26th Symposium British Ecological Society. Edited by A.J. Gray, M.J. Crawley and P.J. Edwards. Blackwell Scientific Publ., Boston, Mass. pp 207-223.

Waughman, G.J., J.R.J. French and K. Jones. 1981. Nitrogen fixation in some terrestrial environments. In: Nitrogen Fixation. Volume 1. Ecology. Edited by W.J. Broughton. Clarendon Press, Oxford. pp 135-192.

Worley, I.A. 1973. The 'black crust' phenomenon in upper Glacier Bay, Alaska. Northwest Sci. 47: 20-29.

7. GENERAL DISCUSSION

The vegetation on the Robson moraines represented three phases of primary succession in the subalpine forest zone of the Canadian Rocky Mountains. The pioneer Hedysarum phase occurred on moraine 8 and was dominated by Hedysarum boreale var. mackenzii, Salix vestita, Salix glauca and Dryas drummondii. The Dryas transition phase occurred on moraines 7 and 5 and was dominated by D. drummondii, H. boreale and S. glauca. Picea engelmannii was beginning to emerge above the Salix on moraine 5. The oldest successional plant community, the Picea phase, was found on recessional moraines 3, 2, and 1 and on the terminal moraine. It was dominated by P. engelmannii, Arctostaphylos rubra, H. boreale, with Brachythecium spp., Cladonia cariosa and C. pyxidata in the ground layer.

Importance-value curves for all the successional communities were essentially linear, fitting the geometric model or niche preemption model (Pielou 1975), which is typical of species poor-communities controlled by a single factor (Giller 1984). The niche preemption model assumes that a small number of abundant species (dominant species) outcompete other species for a large proportion of a limiting resource (Pielou 1975). This conclusion is also supported by the predominance of negative interspecific associations detected by the association index method on the Robson moraines, which indicates that competition may play an important role in structuring the communities throughout the chronosequence. On the intermediate moraines (4 and 5) the DRYAS-HEDYSARUM CT was predominant. Species diversity indices

(Shannon-Wiener Index (H') and Evenness (J')) and the mean stem diameter of Picea engelmannii decreased in this CT. Dryas and Hedysarum patches are coalescing at this phase of succession, and it is probable that these two species inhibit the establishment and growth of other colonists at this stage by outcompeting them for limited resources.

Evidence suggesting that facilitation is an important mechanism of community change on the Robson moraines is the observation that Hedysarum boreale forms centres of establishment for Salix seedlings, for S. glauca and for Picea engelmannii, which become dominant species on the older moraines. However, on the Robson moraines, P. engelmannii does colonize surfaces younger than those occupied by Hedysarum, and can establish on newly exposed surfaces in the Canadian Rocky Mountains within 12-17 years (Heusser 1956). If facilitation is occurring, it is therefore non-obligate and may affect the rate of community development by enrichment of the local substrate with nitrogen (through symbiotic Rhizobium) which could be used for the subsequent growth of associated species, and not direct species replacement in a strict Clementsian sense.

Only an experimental approach will determine whether facilitation is occurring during the early phase of community development on the Robson moraines, and whether inhibition (competition) is occurring during the intermediate phase. The importance of nitrogen in plant community development on the Robson moraines could be examined by fertilizer additions to the moraines which would test whether nitrogen and/or other nutrients were limiting growth (see Lee et al. 1983). The role of facilitation and inhibition on the moraines could also be

examined by transplanting Salix and Picea seedlings in mineral soil at different phases of succession and monitoring the diameter growth of these species. The effect of root competition on Salix and Picea seedling transplants and naturally established seedling could be examined by trenching plots containing these seedlings and removing potential competitors (e.g., Walker and Chapin 1986). However, as Botkin (1981) points out, species removal experiments, to test whether a species facilitates, inhibits or has no effect on another species, involving long-lived forest species will take decades to complete and are thus impractical for individual investigators.

The results of the plotless method of detecting interspecific associations (Chapter 3) showed that there was a predominance of negative associations of species with Hedysarum boreale on the Robson moraines. In contrast, the results of the sample plot method of detecting interspecific associations (Chapter 4) showed that there were more positive associations and fewer negative associations of species with Hedysarum. This apparent contradiction can be explained by comparing the two methods of detecting interspecific associations. The fundamental difference between the two methods is one of scale. To detect a positive interspecific association, plot sampling methods require only that associated species be in close proximity (i.e., in the neighbourhood) of the other species. The limitation of plot sampling to detect interspecific associations is that the outcome of a test is dependent on the size of the sample plot used (Pielou 1974). However, to detect a positive interspecific association employing a plotless method of sampling, the positively associated species must be in physical contact with one another. Thus species which are in the

neighbourhood of one another but not in physical contact with one another would be negatively associated. This is a limitation of the plotless method of sampling to detect positive interspecific associations. For example, Castilleja occidentalis was found to be negatively associated with Hedysarum boreale when sampled by the plotless method of detecting interspecific associations but was found to be positively associated when the plot sample method was used. Castilleja species are known to be hemiparasitic (Lawrence 1971), and haustoria were found attached to the roots of Hedysarum on the Robson moraines. In this case, Castilleja would be expected to be positively associated with its host but not necessarily in physical contact with Hedysarum's above-ground foliage. As discussed earlier, it remains to determine experimentally whether those species found in the neighbourhood of Hedysarum are also positively influenced by Hedysarum.

Reductions in the intensity of the spatial pattern of species occurred with increasing community age and are indicative of community development approaching a steady or stable state (Kershaw 1959; Greig-Smith 1961), during which rates of change are relatively low. However, the number of scales of pattern of each species remained relatively constant and showed no tendency to decrease on the older moraines, which would be expected if community development was approaching a steady state (Kershaw 1959; Greig-Smith 1961). This observation is not consistent with the findings of Sondheim and Standish (1983), that total soil nitrogen and organic carbon levels on the Robson moraines appear to have reached a "temporary steady state" in less than 200 years, during which rates of change are comparatively

slow. Additional evidence to support or reject the steady state hypothesis could be obtained by utilizing Markovian models to examine whether the composition of the seral communities on the Robson moraines approaches a steady state (e.g., Lippe et al. 1985; see Horn 1981 and Usher 1979, 1987).

The legume Hedysarum boreale var. mackenzii was considered to be the major nitrogen-fixing agent on the Robson moraines, contributing 72% of the biologically fixed nitrogen input in the pioneer Hedysarum phase, 79% in the Dryas transition phase and 87% in the Picea phase of community development. The estimated annual nitrogen input from nitrogen fixation decreased approximately 8-fold over the 200 year forest succession. These results are consistent with the trends to be expected in ecological succession by Odum (1969), Vitousek and Reiners (1975), and Gorham et al. (1979). The decline in nitrogen fixation is characteristic of the late stage in community development and could be one mechanism which helps to maintain the steady state in the amount of total soil nitrogen.

It is concluded that while the 200 year old vegetation on the Robson moraines is physiognomically mature, it has not attained all the characteristics expected of a fully mature community. This conclusion is also supported by the absence of some species on the older moraines which are characteristic of old growth forest in the area, such as Cornus canadensis and Pleurozium schreberi. Future changes on the Robson moraines may include increased abundance of Abies lasiocarpa and feather mosses together with soil maturation until, in the absence of fire, and other disturbances, the old growth Picea-Abies forest of the subalpine zone is attained.

7.1 References

Botkin, D.B. 1981. Causality and succession. In: Forest Succession. Concepts and Application. Edited by D.C. West, H.H. Shugart and D.B. Botkin. Springer - Verleg, New York, NY. pp 36-54.

Connell, J.H. and R.O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.

Gorham, E., P.M. Vitousek and W.A. Reiners. 1979. The regulation of chemical budgets over the course of terrestrial ecosystem succession. Ann. Rev. Ecol. Syst. 10: 53-84.

Greig-Smith, P. 1961. Data on pattern within plant communities. II. Ammophila arenaria (L.) Link. J. Ecol. 49: 703-708.

Heusser, C.J. 1956. Post-glacial environments in the Canadian Rocky Mountains. Ecol. Monogr. 26: 263-302.

Giller, P.S. 1984. Community Structure and the Niche. Chapman and Hall, New York, N.Y. 176 pp.

Horn, H.S. 1981. Succession. In: Theoretical Ecology: Principles and Applications. 2nd Ed. Edited by R.M. May. Sinauer Assoc. Inc. Publ., Sunderland, Mass. pp 253-271.

Kershaw, K.A. 1959. An investigation of the structure of a grassland community. II. The pattern of Dactylis glomerata, Lolium perenne and Trifolium repens. III. Discussion and Conclusions. J. Ecol. 47: 31-53.

Lawrence, G.H.M. 1971. Taxonomy of Vascular Plants. The Macmillan Co., Toronto, Ont. 823 pp.

Lee, J.A., R. Harmer and R. Ignaciuk. 1983. Nitrogen as a limiting factor in plant communities. In: Nitrogen as an Ecological Factor. 22nd Symposium British Ecological Soc. Edited by J.A. Lee, S. McNeill and I.H. Rorison. Blackwell Scientific Publ., Boston, Mass. pp 95-112.

Lippe, E., J.T. De Smidt and D.C. Glenn-Lewin. 1985. Markov models and succession: a test from a heathland in the netherlands. J. Ecol. 73: 775-791.

Odum, E.P. 1969. The strategy of ecosystem development. Science 164: 262-270.

Pielou, E.C. 1974. Population and Community Ecology: Principles and Methods. Gordon and Breach Science Publ., New York, N.Y. 424 pp.

Pielou, E.C. 1975. Ecological Diversity. John Wiley and Sons, Toronto, Ont. 165 pp.

Sondheim, M.W. and J.T. Standish. 1983. Numerical analysis of a chronosequence including an assessment of variability. Can. J. Soil Sci. 63: 501-517.

Usher, M.B. 1979. Markovian approaches to ecological succession. J. Animal Ecol. 48: 413-426.

Usher, M.B. 1981. Modelling ecological succession, with particular reference to Markovian models. Vegetatio 46:11-18.

Usher, M.B. 1987. Modelling successional processes in ecosystems. In: Colonization, Succession and Stability. 26th Symposium British Ecological Soc. Edited by A.J. Gray, M.J. Crawley and P.J. Edwards. Blackwell Scientific Publ., Boston, Mass. pp 31-55.

Vitousek, P.M. and W.A. Reiners. 1975. Ecosystem succession and nutrient retention: a hypothesis. Bioscience 25: 376-381.

Walker, L.R. and F.S. Chapin, III. 1986. Physiological controls over seedling growth in primary succession on an Alaskan floodplain. Ecology 67: 1508-1523.

Appendix 1. Photographs of selected sites on the Robson moraines.

Plate 2-12. General view of outwash looking southwest towards Robson Lake in 1963 (above) and 1964 (below). Except for the odd Salix, colonization was still sparse after 21 years. This area was under ice in 1949. This photo point was labeled FP10 on Plate 2-2.

Plate 2-13. View of a macroplot in 1963 (above) and in 1984 (below). Note the colonization of *Dryas drummondii*, *Hedysarum boreale* var. *mackenzii*, and *Salix* over the 21 year period. This area was under ice in 1949. This photo point was labeled FP11 on Plate 2-2.

Plate 2-14. Overview of recessional moraine 5 in 1963 (above) and 1984 (below) from an outcrop east of the moraines. This photo point was labeled FP13 on Plate 2-2.

Plate 2-15. Overall view of recessional moraines 4 and 3 in 1963 (above) and 1984 (below) from an outcrop east of the moraines. This photo point was labeled FP13 on Plate 2-2.

Plate 2-16. View of the east end of recessional moraine 3 and recessional moraines 2 and 1 in the background in 1963 (above) and 1984 (below) from an outcrop east of the moraines. This photo point was labeled FP12 on Plate 2-2.

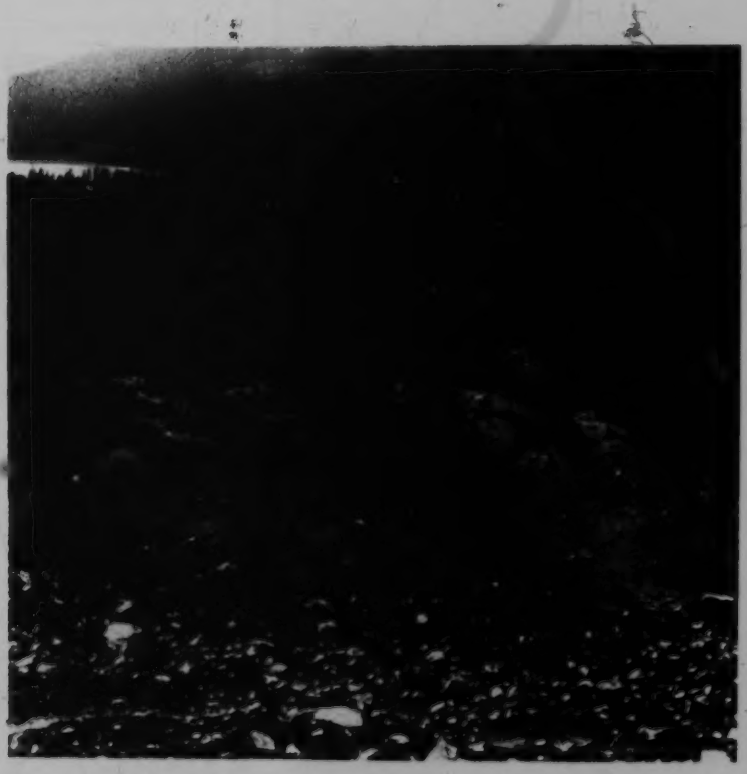
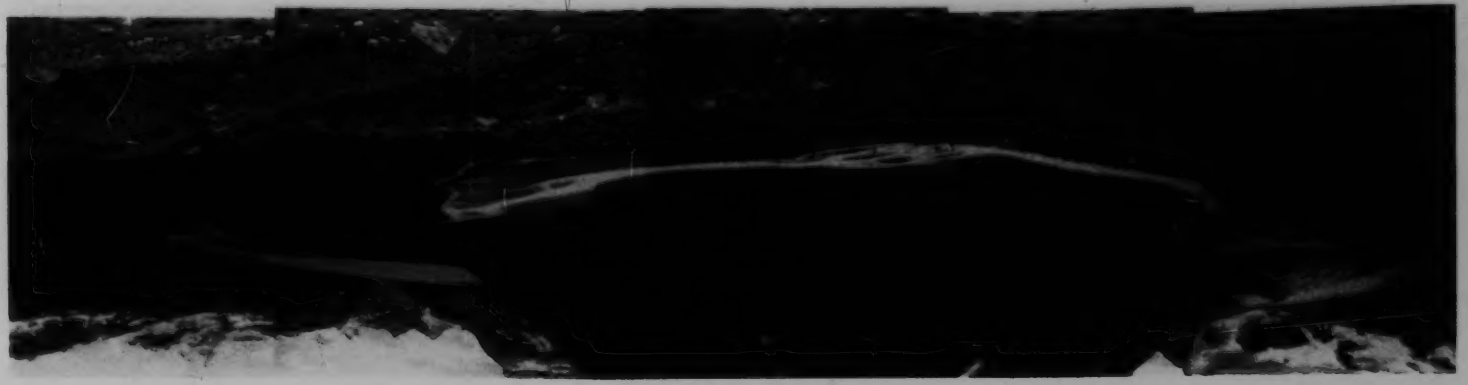


Plate 2-17. Panorama of the Robson moraines in 1984 looking west from the highest point on an outcrop east of the moraines. This photo point was labeled FP14 on Plate 2-2.



Appendix 2. Vegetation data of selected subalpine Picea-Abies forests in the vicinity of the Robson moraines.

Appendix 2. Percentage cover of the species found in selected subalpine Picea-Abies forests in the Robson valley (P = species sampled in the 20 x 20 m plot, cover was <1.0%)

	SUBALPINE FOREST			
LAYER AND SPECIES	Adolphus Lake	Mumm Peak	Rearguard Mountain	Outcrop (adjacent to Robson moraines)
TREE LAYER				
Picea engelmannii	22.0	31.0	38.0	18.0
Abies lasiocarpa	3.0	6.0	2.0	2.0
Pinus albicaulus	1.0	4.0	-	-
TALL SHRUB LAYER				
Picea engelmannii	3.0	-	2.0	-
Abies lasiocarpa	-	-	-	2.0
MID SHRUB LAYER				
Picea engelmannii	-	-	-	0.5
Abies lasiocarpa	-	-	-	13.0
Pinus albicaulus	0.5	-	-	-
Salix vestita	-	-	-	1.0
Salix glauca	-	-	-	P
Salix alaxensis	-	-	-	P
Salix barclayi	-	-	-	P
Salix sp.	-	-	-	P
Betula glandulosa	-	-	-	P
Shepherdia canadensis	-	-	-	P
Rhododendron albiflorum	-	-	-	P
LOW SHRUB LAYER				
Picea engelmannii	P	-	-	-
Abies lasiocarpa	1.0	0.5	0.5	47.0
Salix vestita	-	-	-	1.0
Salix barrattiana	-	-	-	P
Salix sp.	-	-	P	-
Shepherdia canadensis	0.5	0.5	0.5	-
Juniperus communis	2.0	0.5	-	-
Ribes sp.	-	-	0.5	-
Menziesia ferruginea	-	0.5	-	-
Rhododendron albiflorum	-	P	-	-
DWARF SHRUB LAYER				
Picea engelmannii	1.0	-	-	-
Abies lasiocarpa	0.2	0.3	0.7	3.3
Shepherdia canadensis	-	0.1	-	-
Vaccinium caespitosum	0.2	0.4	-	-
Empetrum nigrum	0.6	0.2	-	-
Linnaea borealis	-	2.2	-	-
Phyllodoce empetriformis	-	1.3	-	-
Actaea rubra	-	-	P	-
Cassiope tetragona	-	-	-	P
Arctostaphylos rubra	-	-	P	P

Appendix 2. Continued

LAYER AND SPECIES	SUBALPINE FOREST			
	Adolphus Lake	Mumm Peak	Rearguard Mountain	Outcrop (adjacent to Robson moraines)
FORB-GRAMINOID LAYER				
Thalictrum venulosum	-	1.8	-	-
Artemisia norvegica	1.3	0.7	-	-
Cornus canadensis	2.2	0.5	-	0.1
Listera cordata	0.3	0.2	P	-
Viola orbiculata	1.1	0.1	-	-
Viola adunca	P	-	-	-
Fragaria virginiana	0.5	0.4	-	-
Antennaria neglecta	0.5	2.6	-	-
Erigeron peregrinus	0.7	0.3	-	-
Equisetum scirpoides	0.1	-	0.5	-
Pedicularis bracteosa	1.7	0.4	-	P
Orthilia secunda	-	0.2	0.7	-
Arnica cordifolia	P	0.3	0.5	-
Veratrum viride	-	0.1	-	-
Epilobium angustifolium	P	P	P	-
Pyrola asarifolia	P	0.2	0.5	-
Pyrola secunda	-	-	-	0.4
Pyrola bracteata	-	-	-	0.2
Moneses uniflora	-	-	0.5	0.5
Habenaria viridis	-	-	0.5	-
Goodyera sp.	-	-	0.2	P
Aquilegia flavescens	-	P	-	-
Elymus innovatus	0.5	0.4	-	-
BRYOPHYTE-HEPATIC LAYER				
Pleurozium schreberi	30.3	28.7	0.9	-
Hylocomium splendens	0.2	1.0	80.0	75.0
Drepanocladus uncinatus	7.0	0.4	7.3	22.4
Ptilium crista-castrensis	0.5	3.0	-	-
Dicranum scoparium	-	5.4	P	0.1
Ditrichum flexicaule	P	0.1	-	-
Bryum sp.	-	0.1	0.1	-
Tortula norvegica	-	0.1	-	-
Tortella inclinata	P	-	-	-
Brachythecium sp.	P	-	-	-
Campylium sp.	P	P	-	-
Rhytidiadelphus sp.	-	-	P	-
Barbilophozia lycopodioides	17.4	36.4	8.5	0.2
Lophozia sp.	-	-	-	0.1
Unknown	0.2	-	-	-

Appendix 2. Continued

LAYER AND SPECIES	SUBALPINE FOREST			
	Adolphus Lake	Mumm Peak	Rearguard Mountain	Outcrop (adjacent to Robson moraines)
LICHEN LAYER				
Peltigera aphthosa	2.4	1.1	4.6	0.9
Peltigera canina	-	-	-	0.1
Cladonia pyxidata	P	0.4	P	-
Cladonia sulphurina	-	-	-	P
Cladina mitis	P	-	-	-
Unknown	0.5	0.5	-	-
OTHER				
Bare rock	-	-	-	0.5
Bare soil	-	-	-	-
Litter	42	39	4	5

Appendix 3. Interspecific association data.

Appendix 3. Contingency matrix of interspecific co-occurrences and 'no contacts' (diagonal line) on recessional moraine 8.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
1 Hedysarum boreale	33	3	-	2	-	-	2	-	20	-	-	-	-	6	1	4	1	-	-	2	-	-	-	-	2	9	-
2 Equisetum sp.	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	2	1
3 Saxifraga aizoides	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Castilleja occidentalis	-	-	-	1	-	2	-	-	2	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-
5 Epilobium angustifolium	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Braya humilis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 Poa alpina	1	-	-	-	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
8 Graminoid	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9 Dryas drummondii	15	-	-	-	-	-	-	-	20	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
10 D. octopetala	2	-	-	1	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
11 D. integrifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-
12 Salix reticulata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
13 S. alaxensis	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
14 S. barclayi	5	-	-	-	-	-	-	-	2	-	-	-	-	6	-	2	-	-	-	-	-	-	-	-	1	1	-
15 S. myrtillifolia	3	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
16 S. vestita	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
17 S. barrattiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18 S. ferriae	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19 S. arctica	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
20 S. glauca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-
21 Populus balsamifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
22 Picea engelmannii	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23 Brachythecium sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24 Tortella inclinata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25 Bryum sp.	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26 Ditrichum flexicaule	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
27 Nostoc commune	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 3. (Continued) Contingency matrix of interspecific co-occurrences and 'no contacts' (diagonal line) on recessional moraine 7.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 Hedysarum boreale	5	-	1	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	2	1	6	-	13	-	-
2 Equisetum sp.	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Castilleja occidentalis	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
4 Epilobium latifolium	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Braya humilis	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Poa alpina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 Dryas drummondii	5	1	-	-	-	1	2	1	-	-	4	-	-	-	-	-	-	-	5	4	8	4	5	1	-
8 D. octopetala	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9 D. integrifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
10 Salix alaxensis	1	-	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
11 S. barclayi	8	-	1	-	-	-	3	-	-	-	1	-	2	-	1	-	1	-	1	-	2	-	-	1	-
12 S. myrtillifolia	1	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-
13 S. yestita	4	-	1	-	-	-	-	-	-	-	5	-	-	-	-	-	3	1	-	-	-	-	-	-	-
14 S. barrattiana	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15 S. ferriae	2	-	-	-	-	-	2	-	-	-	-	-	5	-	-	1	-	-	1	-	-	-	1	-	-
16 S. glauca	-	1	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	1	-	-	-	-	-	-
17 Picea engelmannii	1	-	-	-	-	-	-	-	-	1	1	-	4	-	-	-	-	-	-	-	-	-	-	-	-
18 Abies lasiocarpa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19 Brachythecium sp.	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	4	1	-
20 Tortella inclinata	-	1	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	1	1	2	1	-
21 Bryum sp.	-	-	-	-	-	1	2	-	-	-	1	-	-	-	-	-	-	-	1	1	2	1	2	-	-
22 Ditrichum flexicaule	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	1	2	1	1	-	1
23 Tortula norvegica	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	6	-	2	-	-	-	-
24 Campylium sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25 Hypnum revolutum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 3. (Continued) Contingency matrix of interspecific co-occurrences and 'no contacts' (diagonal line) on recessional moraine 5.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
1 Hedysarum boreale	6	-	4	-	6	1	-	-	-	-	-	-	-	-	-	-	-	-	11	2	5	7	20	-	-
2 Epilobium angustifolium	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Fragaria virginiana	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Poa alpina	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5 Dryas drummondii	14	-	1	-	5	1	-	-	-	1	-	-	-	-	-	-	-	-	4	1	8	8	2	1	1
6 D. octopetala	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 D. integrifolia	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
8 Arctostaphylos rubra	-	-	-	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9 Salix alaxensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
10 S. barclayi	5	-	-	-	1	1	-	1	-	1	-	-	-	-	1	-	-	-	2	-	-	1	1	-	-
11 S. myrtillifolia	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
12 S. vestita	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
13 S. ferriae	2	-	-	-	-	-	-	1	-	1	-	-	-	2	-	-	-	1	1	-	-	-	-	-	-
14 S. glauca	7	-	-	-	2	-	-	-	-	4	-	1	-	1	-	-	-	5	-	-	-	-	-	-	-
15 S. scoularia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
16 Populus balsamifera	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17 Shepherdia canadensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
18 Picea engelmannii	2	-	-	-	1	-	-	-	-	2	-	3	3	3	-	-	-	-	-	-	-	-	-	-	-
19 Brachythecium sp.	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1	-	-
20 Tortella inclinata	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
21 Bryum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-
22 Ditrichum flexicaule	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	1	2	-	-	-
23 Tortula norvegica	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	-
24 Amblystegium varium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-
25 Drepanocladus uncinatus	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 3. (Continued) Contingency matric of interspecific co-occurrences and 'no contacts' (diagonal line) on recessional moraine 4.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 Hedysarum boreale	6	-	-	-	6	-	-	2	-	2	-	-	-	-	-	-	-	-	-	11	-	3	2	16	-	-
2 Pedicularis bracteosa	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Castilleja occidentalis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4 Epilobium angustifolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
5 Fragaria virginiana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
6 Pyrola asarifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7 Poa alpina	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-
8 Dryas drummundii	2	-	-	1	3	-	-	-	2	-	-	-	-	-	-	-	-	-	-	3	1	3	1	1	-	-
9 D. octopetala	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
10 Arctostaphylos rubra	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	2	1	1	-
11 A. uva-ursi	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
12 Salix alaxensis	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13 S. barclayi	3	-	-	-	1	-	-	2	-	1	-	1	4	1	1	1	1	-	5	1	-	-	-	2	-	-
14 S. myrtillifolia	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
15 S. vestita	1	1	1	1	-	-	-	-	-	-	-	-	1	1	-	-	1	-	2	-	-	-	-	-	-	-
16 S. ferriae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-
17 S. glauca	2	-	-	-	-	-	-	-	-	-	-	-	1	-	1	1	1	-	1	-	-	-	-	-	-	-
18 Shepherdia canadensis	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-
19 Picea engelmannii	2	-	-	-	-	-	-	-	-	-	-	1	12	-	4	-	-	-	-	-	-	-	-	-	-	-
20 Brachythecium sp.	-	-	-	-	1	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	4	2	-	-	-
21 Tortella inclinata	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	1	1	1	-	2	-	-
22 Bryum sp.	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	4	3	1	4	-	-	-
23 Ditrichum flexicaule	1	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	2	3	6	-	2	-	-
24 Tortula norvegica	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	-
25 Amblystegium varium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
26 Hypnum revolutum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 3. (Continued) Contingency matrix of interspecific co-occurrences and 'no contacts' (diagonal line) on recessional moraine 3.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26
1 Hedysarum boreale	-	-	2	-	-	-	2	2	1	-	-	-	-	-	-	13	2	3	5	16	-	-	-	1	-	-
2 Epilobium angustifolium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3 Fragaria virginiana	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
4 Pyrola asarifolia	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-
5 Graminoid	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6 Dryas drummondii	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	-	2	2	1	-	1	-	-	-	-
7 D. octopetala	2	-	-	1	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	1	-	-	-	-	-	-
8 Arctostaphylos rubra	3	-	-	-	-	-	-	-	-	1	-	-	-	-	-	3	1	1	-	-	-	-	-	-	-	-
9 A. uva-ursi	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
10 Salix barclayi	1	-	-	-	-	-	1	2	-	-	2	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-
11 S. vestita	-	-	-	-	-	-	-	-	-	1	-	1	-	1	1	-	-	-	-	-	-	-	-	-	-	-
12 S. ferriae	-	-	-	-	-	-	-	-	-	2	1	-	-	1	2	1	-	-	-	-	-	-	-	-	-	-
13 S. glauca	2	-	-	-	-	-	-	-	1	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-
14 Shepherdia canadensis	-	-	-	-	-	-	-	-	-	1	1	-	-	-	3	-	-	-	-	-	-	-	-	-	-	-
15 Picea engelmannii	3	-	-	-	-	-	-	2	-	3	4	7	12	3	-	-	-	-	-	-	-	-	-	-	-	-
16 Brachythecium sp.	-	1	1	-	-	-	1	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-
17 Tortella inclinata	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3	3	1	-	-	-	1	-	-
18 Bryum sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	3	2	1	1	-	-	-	-
19 Ditrichum flexicaule	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	2	1	6	-	2	-	-	1	1	-	-
20 Tortula norvegica	2	-	-	-	-	-	-	1	1	-	-	-	-	-	-	2	-	-	-	-	1	-	-	-	-	-
21 Amblystegium varium	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22 Campylium sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23 Hypnum revolutum	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
24 Cladonia sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	1	-	-	-	-	-	-	1
25 Peltigera rufescens	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	1
26 Rinodina turfacea	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Appendix 3. (Continued) Contingency matrix of interspecific co-occurrences and 'no contacts' (diagonal line) on recessional moraine 1.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37
1 Hedysarum boreale	·	·	·	·	·	·	·	·	·	·	4	·	·	·	·	·	·	·	·	·	·	·	·	5	6	·	5	4	·	·	·	·	·	1	·	·	2
2 Botrychium simplex	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
3 Pyrola asarifolia	1	·	·	·	·	·	1	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·
4 Aster sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·
5 Pinguicula vulgaris	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
6 Pedicularis bracteosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
7 Carex concinna	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·
8 Carex scirpoidea	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
9 Dryas octopetala	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	6	·	·	·	·	·	1	1	·	·	1
10 Dryas integrifolia	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·
11 Arctostaphylos rubra	·	·	·	·	1	·	·	1	2	·	1	·	1	·	·	·	·	·	·	·	·	·	·	3	·	·	5	1	1	·	·	·	1	1	·	·	1
12 Salix alaxensis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
13 S. barclayi	1	·	·	·	·	·	·	·	2	·	2	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
14 S. myrtillifolia	·	·	·	·	·	·	·	·	2	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
15 S. vestita	1	·	·	·	·	·	·	1	·	·	1	1	·	·	·	1	·	2	3	·	3	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·
16 S. ferrisae	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
17 S. glauca	·	·	·	·	·	·	·	·	·	·	1	·	·	·	1	1	·	·	1	·	1	·	1	·	·	·	·	·	1	·	·	·	·	·	·	·	·
18 Shepherdia canadensis	1	1	·	·	·	·	·	·	1	·	1	·	·	1	·	2	2	·	3	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
19 Betula glandulosa	·	·	·	·	1	·	·	·	·	·	1	·	3	1	4	·	1	4	·	·	1	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·
20 Juniperus communis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
21 Picea engelmannii	·	·	·	·	·	·	·	·	·	·	1	·	·	1	4	·	·	6	·	1	·	1	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·
22 Abies lasiocarpa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
23 Pinus albicaulis	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
24 Brachythecium sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	·	·	·	·	·	·	·	·	·
25 Tortella inclinata	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	5	1	·	·	·	·	·	2	·	·	·
26 Bryum sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·
27 Ditrichum flexicaule	1	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	2	1	1	1	·	1	·	·	·	7	·	·	·
28 Tortula norvegica	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	1	·	·	·
29 Drepanocladus uncinatus	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·
30 Rhacomitrichum canescens	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
31 Hylocomium splendens	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·
32 Distichium capillacium	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	1	·	·	·	·	·	·	·	·
33 Barbilophozia lycopodioides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
34 Cladonia sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	7	1	·	·	·	·	·	·	·	·	·
35 Peltigera rufescens	·	·	·	·	·	·	·	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
36 Caloplaca sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·
37 Cetraria sp.	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	·	·	·	·	2	·	·	·

Appendix 4. Percentage cover of each species in 600 contiguous 10x10 cm quadrats on transect 2 of recessional moraines 8,7,5,3, and 1. The data are arranged by row from left to right.

HEDYSARUM BOREALE VAR. MACKENZII (MORAINE 8)

000 000 000 000 000 000 000 000 000 000 000 000 0.5 000 0.5 0.5 0.5 010
006 001 000 000 015 005 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 006 002 000 000 000 000 001 035 030 004 000 001 012 030 060 045
008 000 000 000 003 001 002 0.5 000 002 000 000 002 003 007 035 002 000
000 000 000 005 025 035 035 030 030 012 004 000 007 009 017 013 003 0.5
007 0.5 001 000 000 003 001 000 000 000 000 008 003 011 002 000 000 000
001 000 000 000 000 000 000 000 000 000 000 022 050 045 006 000 000 000
000 000 000 003 000 000 000 000 000 000 000 000 000 002 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 003 002 000 000 000 001
000 000 002 001 000 000 0.5 000 000 000 000 003 025 023 027 012 0.5 000
000 000 000 000 000 000 000 000 000 000 000 000 000 010 020 000 0.5 000
000 000 000 004 000 000 0.5 000 000 0.5 0.5 003 000 001 008 0.5 008 000
000 001 001 022 015 000 0.5 000 010 000 002 003 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 002 002 020 050 025 010
000 000 000 000 001 0.5 001 000 000 000 000 000 000 000 000 000 0.5 000
000 000 000 000 000 000 0.5 000 000 000 000 000 010 008 000 000 0.5 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 0.5 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 003 000 000 000 000
000 005 007 003 002 000 001 000 000 000 000 000 001 0.5 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 0.5 000 000 0.5 000 0.5 000 000 000
002 002 000 000 000 000 000 0.5 000 000 0.5 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 0.5 000 000 000 001 000 000 000 000 000 010 007 000 000 000
001 001 0.5 000 000 000 000 000 005 000 000 000 000 000 000 002 000 004
000 000 000 000 000 000 000 018 015 028 000 000 000 004 010 004 004 000
000 010 007 002 000 000 005 007 007 0.5 000 000 000 001 010 070 070 085
060 010 000 000 000 000

HEDYSARUM BOREALE VAR. MACKENZII (MORAINE 7)

000 000 003 002 012 012 008 008 025 013 003 012 020 020 016 018 040 015
006 011 004 000 003 007 014 004 007 025 040 028 020 007 000 003 030 021
013 016 003 005 007 008 000 000 003 013 003 000 006 003 000 0.5 005 007
003 027 011 001 005 004 011 025 002 002 0.5 004 014 000 000 005 017 015
009 014 013 015 012 015 010 002 003 014 021 035 015 017 008 005 003 003
006 005 004 004 003 000 000 000 010 006 012 014 017 017 005 002 001 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 002 000 006 009
011 010 012 004 015 002 000 010 050 000 000 003 004 017 004 007 000 000
001 005 000 0.5 002 009 001 000 000 000 000 003 006 005 000 000 000 000
000 002 000 0.5 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 002 000 003 000 000 000 006 000 000 000 000 000 0.5 0.5 000 000
010 010 003 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 002 000 000 0.5 0.5 000 007 012 0.5 0.5 000 001 007 000 014 005 000
000 002 007 000 000 004 002 005 007 0.5 000 015 017 003 008 003 019 003
006 008 003 011 004 007 000 001 012 007 000 0.5 014 013 013 002 000 000
008 018 010 000 012 011 016 020 014 000 000 000 005 0.5 002 001 007 000
000 000 002 006 000 000 000 003 005 004 001 000 003 010 000 000 007 022
011 012 025 000 000 000 007 005 018 014 009 008 007 015 013 017 015 025
015 000 000 008 004 001 000 000 000 000 000 000 000 000 000 002 008 020
008 002 009 016 022 004 005 007 0.5 001 005 000 000 000 000 012 022 007
000 000 000 010 020 012 001 011 007 000 006 002 012 017 016 017 017 014
000 003 010 015 025 009 020 005 000 004 060 013 001 006 006 001 000 000
000 000 000 000 006 012 007 000 000 007 007 018 020 006 000 007 011 001
0.5 000 000 000 000 000 000 000 000 000 011 017 010 000 023 018 010 005
000 000 002 010 000 008 000 000 000 000 000 000 000 000 025 007 004 002
013 011 000 000 014 007 000 000 006 011 003 012 005 000 004 008 0.5 007
000 000 000 006 020 029 017 003 000 000 001 000 000 000 000 000 000 000
000 000 000 000 000 000 000 0.5 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 015 024 006 000 000 005 003 000 000 000 000 000 000 000
000 000 000 000 000 000 006 018 026 014 003 000 000 000 000 000 000 000
000 000 014 025 024 006 000 000 000 000 000 002 023 014 009 000 000 000
000 002 007 009 015 013 004 000 006 004 022 019 012 013 016 004 000 000
003 004 015 010 008 023

HEDYSARUM BOREALE VAR. MACKENZII (MORAINE 5)

000 004 013 016 019 011 000 004 008 000 005 000 000 005 001 004 005 038
015 008 019 009 018 015 011 009 014 030 002 004 006 004 016 013 016 000
000 005 009 011 018 003 000 003 008 008 004 009 014 000 000 000 009 012
007 018 021 009 014 014 003 016 001 008 008 020 004 014 010 003 000 000
008 016 011 003 009 010 005 004 000 000 000 000 000 000 000 014 030 018
011 003 025 005 006 000 007 004 000 0.5 004 009 014 003 009 009 005 021
015 0.5 003 003 004 002 004 000 003 0.5 000 000 006 009 003 013 0.5 006
000 000 000 000 018 017 000 008 009 025 014 008 010 001 007 022 024 016
019 009 000 009 019 019 007 000 000 000 002 000 004 005 009 007 017 006
016 013 028 030 016 008 017 025 012 0.5 0.5 030 040 009 005 017 003 006
009 003 000 004 017 001 000 000 011 010 015 011 007 002 016 012 000 000
000 012 024 003 008 010 002 000 000 000 000 000 000 002 009 012 020 013
002 013 022 017 005 011 0.5 000 000 000 000 000 000 000 000 000 000 013
017 003 013 009 002 002 008 002 000 000 000 000 003 012 004 000 008 003
003 008 000 000 000 000 002 017 022 006 000 011 021 0.5 000 000 000 000
000 016 017 026 028 018 002 004 003 014 023 012 002 000 000 000 015 017
000 000 007 003 002 000 000 0.5 000 000 000 000 000 008 008 000 000 006
000 000 000 000 000 000 0.5 015 000 006 016 011 005 000 000 0.5 003 006
000 000 010 006 001 008 011 030 014 024 017 012 000 003 013 035 025 009
018 006 005 002 022 027 024 012 013 017 030 018 002 002 000 000 000 000
000 000 012 015 000 005 003 0.5 010 000 011 000 0.5 000 000 000 010 024
018 014 013 0.5 007 009 016 019 000 000 000 007 012 006 003 000 000 0.5
022 010 0.5 000 000 000 000 000 0.5 007 011 010 000 000 002 000 000 007
0.5 000 000 000 001 012 007 030 026 000 000 000 007 000 000 000 009 014
003 000 004 010 010 017 014 001 000 008 022 007 019 008 000 003 008 015
005 000 004 000 012 025 012 000 007 010 002 010 015 030 013 000 000 000
000 001 000 000 000 000 014 009 006 018 017 003 019 015 016 017 008 000
000 000 000 0.5 028 035 035 014 000 006 017 010 0.5 004 008 025 029 016
011 0.5 0.5 011 007 026 044 028 016 012 000 000 000 000 023 015 018 017
033 036 009 030 037 031 005 026 027 004 029 048 018 016 004 008 011 025
020 014 0.5 000 000 0.5 010 000 000 000 017 006 002 025 000 003 000 004
021 000 000 000 0.5 002 011 000 000 000 001 007 005 036 015 015 005 021
019 0.5 024 000 000 009 010 003 002 000 001 013 019 018 039 014 003 000
000 000 000 000 010 045

HEDYSARUM BOREALE VAR. MACKENZII (MORAINE 3)

021 030 008 028 005 012 008 014 015 000 000 000 000 000 000 000 018 008
007 008 017 013 000 000 000 017 014 030 055 015 009 025 000 021 010 007
006 025 020 016 0.5 000 0.5 009 018 000 012 000 000 0.5 0.5 004 022 019
018 022 006 020 036 009 002 002 023 000 013 012 000 009 011 000 020 020
016 030 030 028 008 022 021 000 000 000 003 025 022 006 000 030 035 025
027 0.5 003 024 006 000 000 013 027 022 026 035 020 035 028 037 026 019
021 019 018 003 037 030 018 016 006 018 007 004 001 024 026 009 0.5 000
000 015 008 014 004 000 000 000 000 003 000 004 004 0.5 007 030 026 025
012 012 017 021 014 007 008 001 028 001 001 000 012 000 023 006 012 018
019 009 000 020 024 020 005 003 015 012 009 017 009 000 000 016 015 008
000 004 023 002 000 003 018 018 011 014 007 025 014 014 020 013 013 014
000 000 000 000 000 014 010 002 001 000 001 000 000 010 000 000 019 014
011 010 016 028 025 009 010 027 019 005 000 000 000 000 000 000 009 007
006 000 000 000 000 000 000 005 022 000 000 000 016 012 006 009 010 014
011 015 013 0.5 000 007 007 000 000 000 000 014 025 025 009 000 003 038
036 003 013 018 010 003 012 018 015 002 009 026 021 025 026 013 000 002
000 002 008 000 000 000 015 012 000 003 014 001 000 010 014 003 032 005
000 000 000 012 0.5 000 016 004 001 015 014 000 011 013 015 000 000 000
000 002 008 0.5 024 002 000 000 002 023 027 009 005 029 035 014 027 031
023 038 040 017 000 0.5 000 006 017 030 004 003 000 000 009 005 022 013
010 017 000 0.5 012 007 010 0.5 006 002 013 0.5 003 023 022 032 029 012
005 002 015 025 004 007 031 018 008 027 021 020 000 003 034 017 007 000
000 000 004 009 027 020 002 010 002 000 000 000 000 000 000 000 000 006
000 000 000 006 000 001 000 012 024 010 011 007 000 016 035 034 008 000
004 005 023 032 011 013 037 042 031 026 033 009 001 013 013 029 019 024
015 007 000 000 000 000 003 006 014 037 021 029 019 016 005 000 024 034
036 026 012 000 000 000 000 001 000 000 0.5 015 015 031 025 0.5 013 003
014 014 012 002 001 007 000 013 020 024 016 012 001 000 0.5 000 000 000
000 000 000 000 000 000 000 000 002 020 020 016 0.5 000 000 000 000 000
000 001 007 024 0.5 000 019 008 021 011 027 024 016 009 011 019 033 024
017 0.5 000 014 028 018 014 007 039 001 003 018 014 001 001 011 017 019
020 0.5 001 004 031 020 029 001 006 042 038 034 037 030 022 000 000 000
019 004 014 031 015 022 004 000 000 000 001 008 018 027 020 020 017 027
006 025 029 014 038 044

HEDYSARUM BOREALE VAR. MACKENZII (MORAINE 1)

000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 004 002
0.5 000 000 000 000 003 007 000 000 008 009 000 000 000 000 000 000 000
000 000 000 002 020 009 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 0.5 006 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 001 004 000 000 000 000 000 000 000 000 000
000 000 000 015 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 006 000 011 000
000 000 000 000 000 000 000 000 000 000 000 011 012 001 000 000 000 000
000 014 013 020 005 003 001 010 007 012 011 000 000 000 000 000 000 013
000 000 000 0.5 031 028 001 016 000 006 000 000 017 000 000 000 023 007
000 000 000 000 000 000 012 004 000 000 000 000 000 000 000 000 000 010
025 009 013 007 004 001 019 001 000 000 000 005 014 0.5 000 000 000 000
000 000 000 000 000 000 000 000 001 016 008 002 000 000 000 000 000 000
000 000 004 014 022 018 000 000 008 017 024 012 004 025 010 000 000 000
000 006 018 000 000 000 000 000 000 000 000 000 000 000 000 0.5 0.5 011 019
000 014 003 000 000 000 000 000 000 000 000 000 000 001 019 007 014 000 000
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DRYAS DRUMMONDII (MORAINE 8)

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DRYAS DRUMMONDII (MORAINE 7)

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DRYAS DRUMMONDII (MORAINE 5)

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DRYAS DRUMMONDII (MORAINE 3)

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DRYAS OCTOPETALA (MORAINE 7)

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DRYAS OCTOPETALA (MORAINE 3)

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DRYAS OCTOPETALA (MORAINE 1)

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SALIX GLAUCA (MORAINE 8)

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SALIX GLAUCA (MORAINE 7)

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SALIX GLAUCA (MORAINE 5)

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SALIX GLAUCA (MORAINE 3)

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SALIX GLAUCA (MORAINE 1)

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SALIX VESTITA (MORAINE 8)

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SALIX VESTITA (MORAINE 7)

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SALIX VESTITA (MORAINE 5)

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SALIX VESTITA (MORAINE 3)

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SALIX BARCLAYI (MORAINE 8)

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SALIX BARCLAYI (MORAINE 7)

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SALIX BARCLAYI (MORAINE 5)

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SALIX BARCLAYI (MORAINE 3)

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SALIX BARCLAYI (MORAINE 1)

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ARCTOSTAPHYLOS RUBRA (MORAINE 3)

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ARCTOSTAPHYLOS RUBRA (MORAINE 1)

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PICEA ENGELMANNII (MORAINE 7)

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CLADONIA SP. (MORAINE 7)

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CLADONIA SP. (MORAINE 5)

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CLADONIA SP. (MORAINE 3)

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CLADONIA SP. (MORAINE 1)

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BRACHYTHECIUM SP. (MORAINE 7)

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BRACHYTHECIUM SP. (MORAINE 5)

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030 060 040 022 000 0.5 008 007 006 006 008 0.5 0.5 005 009 008 012 060
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BRACHYTHECIUM SP. (MORAINE 3)

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007 013 007 0.5 003 0.5 0.5 0.5 003 0.5 001 000 000 000 002 0.5 002 004
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026 002 0.5 019 008 006 003 002 010 002 004 0.5 0.5 000 0.5 0.5 005 006
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BRACHYTHECIUM SP. (MORAINE 1)

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BRYUM SP. (MORAINE 8)

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BRYUM SP. (MORAINE 7)

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010 012 012 006 020 008 005 001 005 014 005 012 015 000 0.5 0.5 000 0.5
001 0.5 002 025 022 011 022 017 017 005 012 000 004 0.5 007 017 016 017
010 033 005 020 001 0.5 0.5 0.5 0.5 009 015 023 010 001 002 000 000 000
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000 0.5 004 010 006 002 002 003 001 009 004 0.5 003 006 005 004 004 001
010 002 0.5 001 0.5 0.5 001 002 000 0.5 002 003 000 002 004 0.5 000 000
0.5 0.5 003 000 0.5 0.5 000 000 004 0.5 000 000 006 012 010 003 004 006
009 004 0.5 0.5 000 000 0.5 000 002 004 007 001 004 003 0.5 004 020 000
015 023 002 006 000 009 007 003 003 009 004 013 002 000 002 015 003 000
015 005 0.5 016 006 004 000 0.5 000 000 000 000 0.5 002 003 002 001 0.5
001 001 002 003 005 007 006 003 003 006 010 005 003 002 001 000 000 000
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003 0.5 003 002 000 0.5 000 0.5 004 015 030 0.5 0.5 003 004 025 035 003
002 008 005 015 060 047 008 020 018 016 007 006 014 005 002 004 004 005
0.5 002 021 0.5 008 005 003 003 002 002 0.5 0.5 000 0.5 0.5 000 000 000
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BRYUM SP. (MORAINE 5)

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012 001 002 004 016 010 000 000 015 000 020 019 000 005 002 0.5 004 0.5
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010 003 002 0.5 0.5 000 0.5 000 003 001 001 000 000 000 000 000 001 0.5
0.5 0.5 0.5 003 012 051

BRYUM SP. (MORAINE 3)

005 0.5 005 001 005 001 0.5 002 003 008 009 003 007 007 002 008 005 008
012 0.5 001 002 014 000 001 004 007 005 000 011 010 004 000 0.5 001 001
003 009 003 000 000 000 000 0.5 000 003 004 005 003 007 0.5 000 0.5 0.5 000
000 000 000 0.5 000 004 012 012 008 018 003 004 001 004 006 001 000 0.5
003 007 0.5 000 000 008 035 0.5 001 002 013 0.5 008 014 0.5 000 000 0.5
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048 020 030 035 000 000 000 002 004 0.5 0.5 002 0.5 000 0.5 002 0.5 000
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035 022 007 000 000 0.5 001 020 003 001 006 004 000 0.5 001 006 003 002
008 004 0.5 000 000 000 000 0.5 000 000 0.5 001 0.5 000 000 000 000 000
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008 0.5 002 001 000 000 000 0.5 000 018 033 020 015 006 007 002 018 013
014 016 010 032 016 005 0.5 0.5 0.5 000 000 000 0.5 003 002 000 0.5 000
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008 021 030 035 037 018 028 030 011 013 006 001 006 000 004 003 004 000
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BRYUM SP. (MORAINE 1)

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TORTELLA INCLINATA (MORAINE 7)

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TORTELLA INCLINATA (MORAINE 3)

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TORTELLA INCLINATA (MORAINE 1)

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DITRICHUM FLEXICAULE (MORAINE 8)

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DITRICHUM FLEXICAULE (MORAINE 7)

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DITRICHUM FLEXICAULE (MORAINE 5)

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DITRICHUM FLEXICAULE (MORAINE 3)

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DITRICHUM FLEXICAULE (MORAINE 1)

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010 009 013 033 018 028 021 050 037 015 014 009 010 015 014 009 004 008
001 012 006 030 038 018 005 008 015 003 014 021 037 006 008 015 037 031
026 021 009 003 004 009 013 002 003 013 009 025 001 003 002 0.5 001 004
018 022 011 005 003 004 007 004 003 000 005 000 000 0.5 000 0.5 000 000
000 006 008 029 006 012 004 006 003 019 030 015 022 020 009 001 008 006
030 034 018 009 001 0.5 006 000 001 012 022 016 015 031 043 019 010 014
002 002 009 0.5 024 019 013 001 0.5 001 004 008 005 000 000 000 000 000
000 000 000 000 000 002 006 0.5 0.5 000 0.5 0.5 0.5 004 012 001 0.5 000
001 000 000 000 000 003 0.5 0.5 004 002 000 0.5 004 012 013 0.5 0.5 0.5
018 010 001 003 016 007 0.5 0.5 000 0.5 000 000 000 000 000 001 0.5 000
001 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 000 000 000 0.5 001 0.5 0.5 000 009 002 002 003 004 002 008 015
014 008 005 015 001 003 010 010 0.5 0.5 0.5 003 001 000 005 009 008 012
008 005 004 006 004 000 000 0.5 004 016 022 026 006 007 005 006 007 005
0.5 0.5 008 007 014 008 025 019 011 007 002 002 007 002 000 008 014 028
005 0.5 010 0.5 000 001 0.5 001 009 001 020 006 005 021 023 006 004 008
006 005 006 000 0.5 000 000 0.5 0.5 0.5 000 003 000 000 000 001 003 002
000 001 001 003 009 003 009 015 018 019 002 003 009 003 001 004 013 002
000 000 000 0.5 008 016 005 004 001 005 006 009 007 008 004 0.5 005 009
012 0.5 012 016 017 024 018 046 013 000 000 000 000 0.5 000 000 000 000
000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000 000
000 000 006 000 002 004 001 009 005 006 009 002 000 000 000 001 0.5 001
008 015 006 0.5 0.5 000 000 003 002 0.5 0.5 000 000 000 000 000 000 003
002 003 005 002 000 000